NOV 6 1922

JOURNAL OF ANATOMY

ORIGINALLY THE JOURNAL OF ANATOMY AND PHYSIOLOGY

CONDUCTED ON BEHALF OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND BY

PROFESSOR EDWARD FAWCETT — UNIVERSITY OF BRISTOL
PROFESSOR J. P. HILL — UNIVERSITY OF LONDON
PROFESSOR ARTHUR ROBINSON — UNIVERSITY OF EDINBURGH
PROFESSOR E. BARCLAY-SMITH — UNIVERSITY OF LONDON
PROFESSOR SIR ARTHUR KEITH — ROYAL COLLEGE OF SURGEONS

LINCOLN'S-INN-FIELDS, LONDON, W.C. 2

VOLUME LVI

PARTS III AND IV

APRIL AND JULY 1922

Entered at New York Post Office as Second Class Matter

(All Rights reserved)

CAMBRIDGE UNIVERSITY PRESS
C. F. CLAY, MANAGER
LONDON: FETTER LANE, E.C. 4
also
H. K. LEWIS & CO., LTD., 136, GOWER STREET, LONDON, W.C. 1
WHELDON AND WESLEY, LTD., 28, ESSEX STREET, LONDON, W.C. 2
CHICAGO: THE UNIVERSITY OF CHICAGO PRESS
(AGENTS FOR THE UNITED STATES AND CANADA)
BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.
TOKYO: THE MARUZEN-KABUSHIKI-KAISHA

Price Twenty Shillings net

PRINTED IN GREAT BRITAIN

WHAT ARE VISCERA?

By C. JUDSON HERRICK,

From the Hull Laboratory of Anatomy, The University of Chicago

Words in commonest use are often most difficult of definition. And the projection of an inquiry into new fields is sometimes followed by strange and confusing applications of familiar terms. Certain soft and messy parts of the body we all agree are viscera, the brain has been termed a viscus, but there is also a visceral skeleton sanctioned by hoary usage. Visceral reactions are unconsciously performed; so are many others and some undoubtedly visceral muscles are under voluntary control. Visceral muscles in general are supplied by the sympathetic nervous system, but not the muscles of the visceral skeleton; and what is the sympathetic nervous system?

Our accounts of the visceral nervous system are especially confused, and the reason is obvious—the thing itself is inextricably intertwined with everything else in the body. Descriptive anatomy alone can help but little, though under the guidance of sound physiological analysis it may contribute much. And it is to this phase of the question that I wish to direct attention.

The usual formulation of Bell's law does scant justice to its gifted author's acumen; for Bell not only demonstrated that dorsal roots are sensory and ventral roots motor, but he distinguished a third category of nerve fibres which we would now call visceral. Gaskell later amplified Bell's idea into a four-root scheme of the spinal nerves, somatic and visceral afferent and somatic and visceral efferent. The details of his scheme have been greatly modified, but the fundamental distinction between somatic and visceral systems of nerve components and centres has been more and more evidently justified as time passed on.

Some thirty years ago a group of American zoologists, following lines suggested by Prof. Osborn's work on the amphibian brain, began an analysis of the functional components of the cranial nerves of vertebrates by the microscopic method, which is still in process and is exerting a profound influence. One of the early fruits of these labours was a more accurate description and a clearer analysis of the visceral systems, both peripheral and central. In short, a "visceral brain" can now be recognised and its limits defined and the analysis of its internal structure is far advanced. Appropriate physiological control has been applied and the analysis carried farther in some directions experimentally. The anatomical method can penetrate into some regions not as yet accessible to experiment, for, given an accurate knowledge of the limits and functional values of the primary sensory and motor centres of the brain stem, the further functional connections of these centres can be

deduced as soon as the courses of the related central fiber tracts are adequately known.

These studies have demonstrated a remarkable uniformity of pattern of reflex mechanisms of the head throughout the vertebrate series when viewed broadly, though with great variation in the details, and these modifications present some difficult problems to which specific reference will be made shortly. In view of the divergencies of usage, especially in Europe, which are growing out of the further study of these ambiguous cases, it seems expedient to formulate the views of the so-called American school and some of their implications.

If, now, we look at the matter from the physiological standpoint, it is possible to frame a definition of viscera in general which, though not free from objections and confusing exceptions, is nevertheless serviceable and probably on the whole the most generally useful.

Sherrington, building on the foundation laid by Gaskell, has divided the receptive organs into exteroceptors, interoceptors and proprioceptors. The related afferent nerves and their central connections readily fall into the corresponding classes, and if to each of these systems we join the neuromotor mechanisms most directly related, the way is opened up for a fundamental analysis of all the organs of the body.

The exteroceptors and related neuromotor apparatus are primarily concerned with the adjustment of the body or its members to external conditions. Since this usually involves a change in the relations of the body as a whole to its environment, these systems in the aggregate may be called somatic.

The interoceptors and related neuromotor apparatus, on the other hand, are primarily concerned with internal adjustments of the body, its conservation and reproduction. The mechanisms here employed are, in the main, those classed as viscera in the dissecting room, and, accordingly, these are called the visceral or splanchnic systems.

The proprioceptors ensure the coordinated or synergic action of the motor apparatus. They are internally excited, but not necessarily visceral. By far the larger part of the proprioceptive system is ancillary to the skeletal musculature and is, therefore, somatic in type as we have defined this term. Any proprioceptors which are excited by the action of visceral muscles, by the same token, would have to be classed with the visceral systems.

The distinction here made between somatic and visceral systems of organs is most fundamental. It cuts down through the entire body and conforms as closely as any single criterion can to current usage. Of course, it cannot be applied inflexibly because the body is not made that way and numerous puzzling questions arise in applying this or any other analytic procedure. Moreover, the somatic and visceral systems do not work independently, but each serves the other and structurally they are intimately knit together.

The non-nervous organs of the human body can, for the most part, readily be classified as somatic or visceral in accordance with this principle; but when

the matter is examined comparatively momentous questions arise, for in numerous cases undoubtedly visceral organs of primitive species have, in the course of evolution, assumed somatic functions and conversely. These transformations are often recapitulated in human embryological development, and such organs in the human adult usually bear the hall-marks of their genetic relationships. Now, in the case of primitively visceral structures which have secondarily acquired somatic functions one must choose whether to classify them as visceral along with their homologues in lower forms in accordance with their genetic relationships or as somatic, recognising only their status in the definitive stage. Good arguments can be adduced for both courses.

In the nervous system we always set off a visceral part over against the remainder, but the limits of the visceral system have been variously drawn. The sympathetic ganglionic plexuses are unquestionably visceral by all commonly accepted standards. But how shall we define the sympathetic nervous system? We now know that many efferent fibres which enter these ganglionic plexuses arise within the central nervous system and that some (if not all) of the afferent visceral fibres are outgrowths of neurons of the spinal and cranial ganglia.

In view of the existing confusion[1] it would seem desirable to abandon the term autonomic nervous system altogether, for it has been defined in so many different ways as to have no generally accepted meaning. Let us retain the word sympathetic nervous system in the good old-fashioned sense as the name of that portion of the visceral nervous system which in the gross can be recognised as such. Those visceral ganglionic plexuses which can be separated in the dissecting room from the cranio-spinal nervous system[2] comprise from time immemorial the sympathetic system. So let the matter rest.

In the more precise usage demanded by microscopic anatomy and physiology, the general[3] visceral nervous system will, then, be defined as comprising all of the neurons directly concerned in the reactions of the viscera as here physiologically determined, whether their cell bodies lie in the sympathetic system (in the restricted sense), in the central nervous system, or in the cranio-spinal ganglia. These neurons which form the visceral nervous system can be accurately localised anatomically and their physiological

[1] Ranson, S. W. 1917. "On the use of the word 'sympathetic' in anatomical and physiological nomenclature." *Anat. Rec.* vol. XI. pp. 397–400.

[2] I say cranio-spinal system, instead of the usual term cerebro-spinal system, in the interest of a more consistent nomenclature. If the lower division of the main neural axis (medulla spinalis) is defined in terms of the enclosing skeleton, the upper division, or encephalon, may well be similarly designated. This is especially important in view of the confusion introduced in the BNA tables by a definition of the word cerebrum at variance with both the classical meaning (synonymous with encephalon) and the modern custom of denoting by it the cerebral hemispheres, or these with the thalamus. The designation of the nerves of the head as cerebral nerves in the BNA tables is inconsistent with the definition of cerebrum there adopted and should be avoided. Cranial nerves and cranio-spinal nervous system are satisfactory terms.

[3] General visceral, in distinction from certain highly specialised visceral nervous systems found only in the head.

characters can be determined experimentally. The efferent route of the general visceral system leading away from the cranio-spinal axis is by a two-neuron path, with preganglionic and postganglionic neurons separated by a synapse. The cell bodies of the afferent neurons lie chiefly (perhaps wholly) in the cranio-spinal ganglia. The peripheral ganglionic plexuses, such as the myenteric and submucous plexuses, are of course included in the general visceral system.

It is common practice nowadays to enlarge the ancient meaning of the word sympathetic system to include all neurons in their entirety which lie wholly or in part in the peripheral sympathetic nervous system in the narrower sense above defined. Here would then be included neurons which lie wholly in sympathetic ganglionic plexuses, preganglionic neurons whose cell bodies lie in the spinal cord and brain and whose axons enter rami communicantes, and also those neurons of spinal and cranial ganglia whose peripheral processes pass out into rami communicantes. This would not be objectionable if the prevailing ambiguity in the use of the term sympathetic could be avoided.

Langley limits the term sympathetic to the efferent elements of the thoracic-lumbar visceral system and applies the term autonomic to the efferent cranio-spinal visceral system as a whole. Certain continental writers, on the other hand, restrict the term autonomic to the cranio-sacral efferent visceral system in contact with the thoracic-lumbar. Still other variant usages are current, and the confusion is so great that some physiologists advise that the terms autonomic, sympathetic and para-sympathetic be eliminated from our nomenclature altogether. If, however, the preganglionic efferent neurons are included in the enlarged definition of the sympathetic system, then the visceral sensory neurons of the spinal ganglia whose peripheral processes enter the rami communicantes should also be included.

In the head the situation is far more complex than in the trunk. Here, in addition to general visceral organ systems arranged essentially as in the trunk, there are special systems concerned primarily with feeding and respiration. These physiologically are intermediate between the general visceral and the somatic organs, for they are concerned with the incorporation into the body of materials from outside. It is, therefore, not surprising to find that structurally also, they occupy an intermediate position.

The bony framework of the jaws, hyoid and branchial arches (and their derivatives in adult mammals) constitutes a true visceral skeleton, as has long been recognised. The related muscles are striated and voluntary and their nerves are in no way related with the sympathetic nervous system. The muscles of the jaws, hyoid and branchial arches were clearly primitively visceral (but neither non-striated or supplied by sympathetic neurons), though the jaws as prehensile organs are also none the less truly somatic. Some of the muscles derived from the embryonic musculature of the visceral arches persist as visceral in the adult man. Others have secondarily acquired typical somatic functions, such as those of the larynx and the mimetic facial musculature, and there is certainly room for difference of opinion as to their

classification. In the current American usage these muscles and their nerves are usually called special visceral in conformity with their genetic relationships. Certain English anatomists, on the other hand, have called them special somatic muscles in accordance with their functional and (adult) anatomical characteristics. This difference in nomenclature is a matter of small importance, for the muscles do occupy an ambiguous position (compare the variability of striation in the oesophageal musculature). The essential thing is the recognition of their *special* character, in contrast with both the general visceral and the typical somatic neuro-muscular systems.

In all vertebrate animals the muscles of this special series in the head are supplied by motor nerves arising from the brain in a lateral series (V, VII, IX, X and XI pairs), clearly separated from the more ventral nerves of the somatic muscles (III, IV, VI and XII pairs). This topographic separation of the somatic and visceral series of motor nerves at their superficial origins applies also to their nuclei of origin in the brain stem, and the intracranial centres of the somatic and visceral sensory systems are similarly distinct. In human embryos and in the adults of the more generalised fishes, where these primary sensory and motor centres make up the greater part of the medulla oblongata, this part of the brain is obviously divisible on each side into four well defined longitudinal columns whose characters are determined chiefly by their peripheral connections. Enumerating them from ventral to dorsal borders, these columns are: somatic motor, visceral motor, visceral sensory, and somatic sensory. To these primitive sensori-motor centres there is added in the adult human brain a much larger volume of correlation mechanisms and long conduction paths, such as the olives, pons, pyramidal tracts, etc.

This method of analysis of the bewildering complexity of the human brain has so clarified the subject that it has been widely adopted, and its pedagogic value has been tested with thousands of medical students. A number of years ago the late Prof. Edinger wrote me with reference to it that he saw its merit, but added: "I fear I am too old a dog to learn the new tricks." But Edinger was of the type that does not grow old, and a few months later I was interested to notice that this plan in its essential features appeared in the next edition of his *Vorlesungen*.

Largely by the comparative study of the functional composition of the cranial nerves and their centres the morphological pattern of the medulla oblongata has been definitely established, and this pattern is found to be in fundamentals surprisingly uniform throughout the vertebrate series. It is always recognisable, even when distorted by exaggerated development of certain systems to a degree almost unbelievable in some species of fishes.

In the higher levels of the brain, where correlation tissue so largely overshadows the primary sensori-motor apparatus, the application of these principles becomes naturally more difficult, and here there is room for wide divergence of opinion and usage.

Let us now turn to a more detailed consideration of some of these puzzling

cases where secondary changes have led to confusion of somatic and visceral types of structure. No simple arbitrary standards can be established for these organs. Their phylogeny, ontogeny, structure and function must be analysed and each treated on its own merits. Uniformity of usage is probably not possible here, for each student will evaluate these matters in accordance with his own ideas of fitness. The principles already laid down can, however, readily be applied as soon as all the necessary facts are known.

Seeking and capturing food is obviously a somatic reaction, but mastication, insalivation, swallowing, and further treatment of this food equally clearly must be classed as visceral, and the mechanisms employed are viscera. Taste is a visceral sense as truly as is hunger, though it is reckoned as a special sense. Its nerves peripherally have no connection with the sympathetic nervous system, but the primary centre for taste in the medulla oblongata is anatomically intimately joined (in the nucleus of the solitary bundle) with the centres for hunger and other visceral senses served by the vagus.

But where taste buds are developed both in the mouth and in the outer skin, as in the carp and catfish, the cutaneous organs of taste at once become exteroceptors and, as we know from experiment, they are used in the search for food and they call forth somatic reactions. This is a secondary or derived condition, for the internal (visceral) taste buds are more primitive than the external. In the catfish the primitive visceral gustatory centre for mouth-tasting is a greatly enlarged portion of the nucleus of the solitary bundle known (somewhat inappropriately) as the vagal lobe. In front of this lobe there is another gustatory centre which is likewise an enlargement of the nucleus of the solitary bundle and is termed (quite properly) the facial lobe, for it receives all of the fibers from the cutaneous taste buds, which enter the brain through the facial nerve. The facial lobe is, therefore, a somatic sensory centre by a strict application of our formula. It is, however, genetically derived from the nucleus of the solitary bundle, a visceral centre, and it is functionally so intimately bound up with the sense of taste served by the internal taste buds that it has usually been termed visceral. In the codfish I have described a very similar situation, where the somatic nature of the centre for cutaneous taste buds is much more clearly evident both structurally and physiologically. Thus, though taste is primitively and typically a visceral sense, it may in some animals acquire somatic characters and develop end-organs and intracranial centres of somatic type.

The sense of smell presents a still more puzzling case, for its twofold nature is always in evidence in all classes of vertebrates. The phylogenetic origin of the organs of taste and smell is obscure, for there are no extant documents which preserve for us the details of their history. In all living vertebrates smell, whatever its origin, is a true exteroceptive sense, concerned with locating objects at a distance and calling forth locomotor reactions of a somatic type. This is the dominant function throughout the vertebrate phylum. Nevertheless there is a visceral phase of olfactory reactions equally widespread and

probably more primitive, namely, their part in the processes of internal preparation of food, such as the excitation of jaw-movements, flow of saliva, etc. This question I have examined in some detail in 1908[1] and I have more recently[2] endeavoured to show that with the opening of the posterior nasal aperture in air breathing vertebrates the visceral or "mouth-smelling" function of the nose took on a new phase with which was correlated the development of the vomero-nasal organ (of Jacobson) and its cerebral centres, the accessory olfactory bulb and amygdala. So intimately bound together, however, are the somatic and visceral functions of the nose that we ourselves are incapable of determining without special laboratory tests whether we are smelling or tasting various articles of food.

In the interest of an adequate understanding of the olfactory organ and the related neuromotor apparatus it is indispensable that these two phases of its functional activity be clearly apprehended. Whether it be called a visceral or a somatic organ is not of so much consequence, for clearly it is both, that is, it is viscero-somatic.

The respiratory mechanisms present another interesting series of transformations which have caused confusion. In fishes the gills are obviously visceral structures concerned primarily with respiration, with an important part to play in the feeding reactions also. Their muscles, unlike the visceral muscles of the trunk, are striated and are not supplied by sympathetic nerves. In mammalian embryos the branchial apparatus, after passing through an ichthyopsid stage, is highly modified in most diverse ways, some parts retaining visceral functions and others, like the larynx, acquiring typical somatic characters. Whether these latter are classed as somatic or visceral will depend upon whether emphasis is placed upon adult relations or upon embryologic or phylogenetic origin. The current American usage, which classes the gills and all their derivatives as visceral, has the merit of simplicity, but requires some explanation and qualification as applied in the human body.

In the course of the transition from water breathing to air breathing vertebrates an entirely new respiratory mechanism was developed, largely from pre-existing skeletal muscles of the thoracic region. Genetically these muscles are somatic and they are commonly so classified. The primary innervation of these muscles of the somatic type from the spinal cord was preserved. But it is interesting to note that the respiratory centre which controls the rhythm of breathing, even in man, does not lie in the spinal cord in relation with the sources of the phrenic and intercostal nerves, but is retained in the vagus region of the lower medulla oblongata, its primitive position in fishes where branchial breathing is in vogue. The appropriation for respiratory purposes of certain structures innervated from the spinal cord has not in-

[1] Herrick, C. Judson. 1908. "On the phylogenetic differentiation of the organs of smell and taste." *Jour. Comp. Neur.* vol. XVIII. pp. 157–166. In this paper will be found also references to the original sources of the statements made above relating to the gustatory centres of fishes.

[2] Herrick, C. Judson. 1921. "The connections of the vomero-nasal nerve, accessory olfactory bulb and amygdala in Amphibia." *Jour. Comp. Neur.* vol. XXXIII. pp. 213–280.

volved the abandonment of the primitive visceral respiratory centre in the brain.

The most extreme instances of secondary transformation of a primitive visceral neuromotor apparatus is perhaps furnished by the spinal accessory nerve and the related trapezius and sternocleidomastoid muscles. These are apparently typical somatic muscles, and their innervation from the lateral or special visceral motor centres presents a serious problem which has been resolved by an application of the comparative method.

The trapezius muscle is found in most groups of vertebrates, though sometimes called by different names (levator scapulae, humeromastoid, cucullaris, capiti-dorso-clavicularis, etc.), and often more or less united with the sternocleidomastoid. The muscles of this group are regarded by comparative anatomists as partially homologous throughout the vertebrate series. They typically have a double innervation, partly from the XI (or X) cranial nerves and partly from the spinal nerves. In elasmobranchs the trapezius muscle is supplied by the "accessorius" branch of the vagus[1] and is regarded by Vetter as a derivative of the superficial constrictor system of the gill region, whose function is to contract the gill chamber. In teleosts the muscle named trapezius is, in some species, innervated from the X cranial nerve and in other species from the spinals. It is probable that two muscles morphologically distinct are combined in the trapezius of higher vertebrates where both innervations occur.

The trapezius is developed in Scyllium, Gallus and Lepus[2] from the mesoderm of the gill arches. In Teleostemi, Ceratodus and Amphibia it is differentiated from the levatores arcuum branchialium and this is regarded by Edgeworth as the primitive condition. Its materials are derived embryologically from the mesoderm of five branchial arches in Scyllium, four in Chrysemys, two in Gallus and three in Lepus.

Kappers[3] in discussing the relations of the spinal accessory nerve shows that both phylogenetically and embryologically (in the sheep) the nucleus of this nerve as seen in the mammals is independent of both the ventral gray column of the spinal cord and the nucleus ambiguus of the medulla oblongata, with both of which it has in the past often been related. The same relations have since been described in the new-born human[4].

In fishes there has usually been described a single large-celled motor vagus nucleus under the name nucleus ambiguus, from the caudal end of which the fibres for the trapezius muscle are derived, in cases where this muscle is inner-

[1] Fürbringer, M. 1897. "Spino-occipitale Nerven." *Festschr. f. Gegenbaur*, Bd. III. Norris and Hughes. 1920. "The cranial, occipital and anterior spinal nerves of the dogfish, *Squalus acanthias*." *Jour. Comp. Neur.* vol. XXXI. pp. 293–402.

[2] Edgeworth, F. H. 1911. "On the morphology of the cranial muscles in some vertebrates." *Q.J.M.S.* vol. LVI. pp. 167–316.

[3] Kappers, C. U. A. 1912. "Weitere Mitteilungen über Neurobiotaxis." VII. *Folia Neurobiol.* Erg.-Heft 6, pp. 3–142.

[4] Black, D. Davidson. 1914. "On the so-called 'bulbar' portion of the accessory nerve." *Anat. Rec.* vol. VIII. pp. 110–112.

vated from the vagus. In the carp[1] and probably in other fishes there is also a dorsal small-celled motor vagus nucleus. This more dorsal nucleus, which forms the motor layer of the vagal lobe, probably as in mammals supplies smooth visceral muscle fibres through the sympathetic nervous system, while the large-celled motor nucleus is known to supply the striated branchial musculature, including the trapezius when present.

The large-celled motor vagus nucleus lies much farther dorsally in fishes than in mammals and is called the dorsal vagus nucleus by Kappers. It is possible that in most fishes and amphibians the true dorsal nucleus is united with the large-celled nucleus to form the "dorsal nucleus" of Kappers, though in the carp, where the vagus is greatly enlarged, the two motor vagus nuclei are clearly separate. The "dorsal vagus nucleus" of Kappers in fishes occupies a position corresponding with that of the dorsal small-celled (general visceral) nucleus in mammals, and Kappers shows that in the phylogenetic series from fishes to mammals there has been a migration ventralward from this "dorsal" nucleus in two directions, one forward and downward to form the nucleus ambiguus supplying the striated muscles of the pharynx and larynx, and one backward and downward to form the accessorius nucleus (spinal nucleus of the XI nerve).

It seems probable, therefore, that the trapezius (or that portion of it in higher vertebrates which is innervated from the XI cranial nerve) was originally a respiratory muscle. The same holds true for the sternocleidomastoid, which has a similar double innervation.

In Sauropsida and Mammalia the demand for greater mobility of the shoulder has apparently incorporated the trapezius and sternocleidomastoid muscles into the complex connected with the shoulder girdle for participation in general shoulder and arm movements. Nevertheless in mammals the respiratory function of these muscles has not been entirely lost. Their twofold relationships were clearly pointed out by Charles Bell[2], and this has since been many times confirmed. Bell reports the case of a hemiplegic who was quite unable to elevate the shoulder on the affected side by an act of will, but who was able in forced inspiration to elevate both shoulders equally, the respiratory function of the trapezius being unimpaired by the failure of the other functions.

Our conclusion is that the trapezius muscle (and the sternocleidomastoid, which appears to have a common origin with it) is in part a derivative of the branchial musculature of primitive fishes, originally respiratory in function. In some fishes it derives its motor innervation from the lower vagal region and this innervation persists in all higher animals.

In Sauropsida and Mammalia, however, a union of the primitive trapezius, of branchial origin innervated from the vagus region, with a slip of the dorsal

[1] Herrick, C. Judson. 1915. "The central gustatory paths in the brains of bony fishes." *Jour. Comp. Neur.* vol. xv. pp. 375–456.

[2] *Phil. Trans.* 1822, pp. 284–312; and *The Nervous System*, 3rd ed. 1844.

musculature innervated from the spinals took place for the double purpose of facilitating movements of the shoulder (with the head fixed) and of the head and respiratory muscles (with the shoulder fixed). The former (which is the dominant function) is a typical somatic movement, and to bring the nucleus of origin of the trapezius muscle into closer relations with the other motor nerves involved in the synergic muscular complex of the shoulder the nucleus of the XI nerve in the course of vertebrate phylogeny has migrated backward into the cervical spinal cord, this being an illustration of Kapper's principle of neurobiotaxis. During this evolution, however, the connection of the trapezius and sternocleidomastoid muscles with the central mechanism of respiration was not lost, and both of these muscles may cooperate as important accessory muscles of respiration. The somatic and visceral (respiratory) functions have separate central nervous pathways leading into the nucleus of the accessorius, and of these the respiratory may be left intact after the loss of the more recently acquired voluntary motor path in certain cases of hemiplegia.

We conclude, then, that in a functional analysis of the animal body three classes of organs must be recognised: (1) visceral, (2) somatic, and (3) ambiguous or transmutant cases, in origin belonging to one of the two primary types but secondarily transformed wholly or in part into the other. The third class cannot be eliminated or ignored, for organisms are not static, but are ever in flux and old materials may be transformed and put to new uses quite at variance with any formal rules which we may lay down in our logical systems.

THE MISUSE OF THE TERM "VISCERAL"[1]

By RAYMOND A. DART, M.Sc., M.B., Ch.M.,
Senior Demonstrator of Anatomy; University College, University of London

INTRODUCTION

"What names are applied to these systems is a relatively unimportant matter, but it is necessary to bear in mind that the olfactory system itself is a complex in which visceral (interoceptive) and somatic (exteroceptive) elements are always present. To deny or ignore this dual nature of the sense of smell is to close the door to further progress." (Herrick, *Jour. of Comp. Neur.* 1921.)

That inherent qualities do not necessarily find expression in terminology is a fact of which men had long been cognisant before Shakespeare delivered himself of his immortal statement concerning the independence of "sweetness" and nomenclature. But such is the limitation of the scientific method that we may only proceed from definition to definition, so names are apt to assume an exaggerated importance and often become the index of the exactitude of our information or of the clearness of our thinking.

In a previous publication (1921) I dissented from the teaching, current amongst certain neurologists, that "smell" is a "specialised visceral sense" and insisted that it was "a thorough-going somatic, ectodermal and exteroceptive sense." In view of Herrick's restatement of the situation, it will be the purpose of this paper to trace briefly the outstanding historical incidents in the production of a glaring confusion in modern neurological and physiological literature, arising out of an unrestrained use of the term "visceral."

The confusion is one of gradual growth. The term "visceral," as first utilised in anatomical literature, was undoubtedly in the adjectival sense of "pertaining to a viscus" (*L. visceralis*), and it is in this original sense that time has justified its use in general anatomical description as opposed to "parietal"—in referring, for example, to the reflections of the abdominal or of the pleural serosa. Further, the term "visceral," as applied to the unstriated, endodermal musculature of the gut or of the other viscera, has afforded, in the past, a suitable distinction between this musculature and that which causes erection of the hair, etc.—the so-called "dermal" (ectodermal) musculature. Although both systems of musculature are innervated and controlled by the vegetative nervous system (systema nervorum sympatheticum) and consequently form a physiological unity, it is true that for descriptive purposes the antithetical character of the two germ layers provided a sufficiently valid phylogenetic background for such a distinction.

[1] Editorial Note. This paper was received by the acting editor, Feb. 9th, 1922. Sixteen days later Prof. Herrick's welcome article (p. 167), dealing with the same subject, arrived, the covering letter bearing the date Feb. 10th, 1922.

The Term "Visceral" in the Skeletal System

An entirely theoretical and artificial force, however, was given to the designation with the appearance of C. Reichert's (1836) inaugural dissertation, "de embryonum arcubus sic dictis branchialibus." To H. Rathke (1825) is due the discovery of the "branchial arch mechanism" in mammalia. This publication together with his succeeding papers (1828–1832) established beyond all question the validity of his contention concerning the presence of the "gill-arch mechanism" in Amniota and by him it was correctly described as "Kiemenapparat." Reichert extended the observations of Rathke; but, being dominated by the conception that "die Visceralhöhle des Kopfes aus Bogen gebildet werde," he re-named the "*branchial arches*" of his far-sighted predecessor "*visceral arches*" (Visceralbogen) purely because of their adaptation to what he was pleased to term the "visceral cavity of the head."

This use of the term "visceral" has become fairly firmly grounded in osteological literature because it afforded a convenient distinction between the cranial skeletal elements developed in apparent adaptation to the digestive tube and its requirements (viscero-cranium) and those in adaptation to the sense organs and the neural tube (neuro-cranium). The distinction so clearly embodied in the work of Reichert, was rendered classical by Huxley's famous Croonian Lecture (1858). Through the advances in morphological interpretation made by Gegenbaur and so many others, it was crystallised in Gaupp's account of the comparative anatomy of the skull. (Hertwig's *Entwickelungslehre*, 1906.)

Valuable as the distinction drawn by Reichert certainly is, it is equally valid to regard, with Gegenbaur, the ribs and other skeletal parts, which are developed for the protection of the gut, as "visceral." This is the accepted terminology in certain quarters, for Dorland's *Medical Dictionary* tells us that the "visceral" skeleton is "that portion of the skeleton which protects the viscera, as the sternum, ribs and innominate bones." It remains to be demonstrated that such a teaching is groundless. Hence it is unfortunate that the term "visceral" should have been selected by Reichert, or that the wider application of his principle should not have been met by suitable adjustments in the nomenclature used by his successors. In the sense of Reichert (as interpreted by Gegenbaur) the "parietally" situated ribs should be called "visceral" structures. Further, the admirable summary of Landacre (1921) and the experimental work of Stone (1921) have clinched a dramatic series of brilliant researches by many workers demonstrating that the so-called "visceral" arches themselves are "dermal" (ectodermal) in origin.

Sufficient will have been said to indicate the deplorable inadequacy of the term "visceral" in osteological literature and to justify a rigid adherence to the fundamental and earlier classification of Rathke where the cranium is concerned.

The Term "Visceral" in the Muscular System

For the next important application of this word in terminology we must note the appearance of Schneider's (1879) early attempt at a comparative myology of Chordata, because it formed the then accepted, though erroneous basis upon which Gaskell later built up his morphological scheme. Schneider divided the musculature of Chordata into the *smooth* and *striated* varieties quite correctly; but he sub-divided the striated musculature into two subsidiary groupings, viz. body or "parietal" musculature and "visceral" musculature. His division is based apparently on the statements: (p. 59) "Die visceralen Muskeln sind die Muskeln der Kiemen, des Kopfes, Mundes, des Velum, der Zunge; man kann sie als die Fortsetzung der glatter Muskelfasern des Darmes betrachten. Beide entstehen aus derselben Schicht."

Such a classification should include all musculature innervated by cranial motor nerves and an appreciable part of the neck musculature also. But Schneider is not obstinate in his contention. He finds (p. 116) that the so-called sterno-pharyngeal muscles of Ganoids and Teleosts are "parietal" muscles. Nevertheless, "Sie entsprechen den Sterno-branchiales, welche wir weiter unten auch bei den Elasmobranchiern finden werden, und dort gehören sie nachweisbar zur *visceralen* Muskulatur." When he comes to deal with amphibian, reptilian and avian forms he is far from confining his "visceral" terminology either to the head and tongue region or even to the limits of his embryological conception, but includes under that heading the Transversus groups (pp. 134, 137, 142, etc.) and the diaphragm.

Such a classification, lacking even in internal harmony, is morphologically worthless. It was unfortunate that Gaskell (1908) should have regarded Schneider's proposals so seriously. Not appreciating the whole extent of the flaws, he seized upon the conception as an elucidation of his theory of vertebrate origin and strove to harmonise this faulty division with van Wijhe's discoveries concerning the segmentation of the Selachian head. When Gaskell differed from Schneider by restricting the term "visceral" to the branchial musculature, his use of the term might have been expected to apply to all of the musculature attached to the skeletal elements described by Reichert as "visceral." This was not so, for in order to adapt it to his theory, Gaskell (p. 172) separated out the hypoglossal musculature as a "spinal somatic" and the eye musculature as a "cranial somatic" group. According to him, these were the only muscles innervated by cranial nerves which were at all comparable with the other striated muscles of the body, forming with them the "somatic" as opposed to the "visceral" musculature.

Quite apart from the philological objection to an antithesis of Greek and Latin terms, the artificiality of Gaskell's arrangement of the musculature constitutes sufficient reason for not adopting it, for it is at variance with the embryological evidence, which it was supposed to elucidate.

If we trace the history of embryological terminology this is abundantly

clear. We find that Pander (1817) was the first to distinguish clearly the three-layered blastoderm in the following terms: "serous" or outer, "vascular" or middle and "mucous" or inner. Shortly afterwards Von Baer substituted the terms "animal" and "vegetative" for the outer and inner layers respectively, and did not recognise the middle layer as a separate entity. Remak, however (1850–1855), reverted to the conception of Pander in a modified form, calling attention to the morphological significance of the "split" in the middle layer, whereby the coelomic space is formed and is so bounded externally in the embryo by a "Hautfaserblatt" and internally by the "Darmfaserblatt." The two mesodermal layers became known as the "somatopleure" and "splanchnopleure" respectively, and the terms were established in embryological literature by Balfour's work (1885) as the "*somatic*" and "*splanchnic*" layers. Meantime, in the year when Darwin's *Origin of Species* appeared, the genius of Huxley (1859) elucidated the homology of Pander's serous and mucous layers in Mammalia with the "ectoderm" and "endoderm" of Coelenterata. The year 1859 consequently saw a complete basis provided for embryological generalisation.

The embryological facts concerning the origin of striated muscles were tersely stated by Balfour (*loc. cit.* p. 671) as follows: "The first changes of the mesoblastic somites and the formation of the muscle-plates do not, according to existing statements take place on quite the same type throughout the Vertebrata, yet the comparison which has been instituted between Elasmobranchs and other Vertebrata appears to prove that there are important common features in their development, which may be regarded as primitive, and as having been inherited from the ancestors of Vertebrata. These features are (1) the extension of the body cavity into the vertebral plates, and subsequent enclosure of this cavity between the two layers of the muscle plates; (2) the primitive division of the vertebral plate into an outer (somatic) and an inner (splanchnic) layer, and the formation of a large part of the voluntary system out of the inner layer, which in all cases is converted into muscles earlier than the outer layer."

And p. 673: "Thus both layers of the muscle plate are concerned in forming the great longitudinal lateral muscles, though the splanchnic layer is converted into muscles very much sooner than the somatic."

The Hertwigs, Rabl and Maurer go even further and state that the whole of the "parietal" musculature arises from the inner or "splanchnic" layer of the somite.

The first consideration that emerges from these statements is that all somites are homologous in giving rise to striated ("parietal," "somatic") musculature from the medial or "splanchnic" lamella; consequently the term "splanchnic" as used by Balfour in embryology cannot be correlated in any way with "visceral" (its Latin translation) as employed by Gaskell. Secondly, it is no distinctive feature of the "branchial" musculature (as Maurer, *Hertwig's Entwickelungslehre*, p. 47, appears to believe) that "Aus dieser medialen

Lamelle welche der Splanchnopleura entspricht, bildet sich die Muskulatur der einzelnen Kiemenbogen aus."

It would be entirely misleading to assume that the embryologists of the same period (Cf. Maurer, *loc. cit.*) were in harmony with Gaskell's arbitrary division of the cranial musculature. Hatschek, with admirable penetration, recognised that if the musculature of the branchial arches was to be called "visceral" then the embryologically homologous muscles supplied by the oculomotor and abducens nerves are "visceral," a view which Maurer himself extends to the trochlear muscles as well. All of these muscles have their origin in somites—somites which, in certain cases, are giving rise simultaneously to musculature (e.g. masticatory muscles) that is *visceral* in the senses of both Reichert and Gaskell. The same mesodermal origin is so well known in the case of the striated musculature innervated by the glossopharyngeal, vagus, accessory and hypoglossal nerves, that to mention it is to become trite—all belongs embryologically to the type called *somatic* by Gaskell.

The only rational way in which the term "visceral" could possibly be applied to a portion of the striated musculature (and then only as a descriptive term), is in the sense defined by Reichert, where it is synonymous with the term "branchial," as was first clearly indicated by the researches of Rathke on the "Kiemenapparat." Even so, the term introduced by Reichert is objectionable as applied to the musculature, because it tends to exaggerate the real distinction between the gill-arch musculature and the general body musculature. Consequently the discarding of this application of the word would eliminate an element of confusion from the literature relating to the striated musculature. The descriptive, and earlier, term "branchial" (of Rathke) is not open to this objection; but it, too, is of value only as long as the embryologically homologous character of all muscles with the visual muscles on the one hand, and with the so-called parietal muscles on the other, are clearly recognised. Since all of these are now known to arise from segmented mesoderm, they may be grouped together morphologically as the *mesodermal* musculature.

It must not be presumed that, in criticising Gaskell's division of the striated musculature, any attempt is being made to minimise the emphasis which his work placed upon the fundamental anatomical and physiological distinction to be drawn between the *striated* and *unstriated* musculature. However clearly anatomists had recognised the distinction between the two systems, it remained for Gaskell and his followers in physiology—more especially Cannon—to provide the evidence necessary to show that the involuntary unstriated musculature, with its characteristic innervation, presented a unity phylogenetically older and more widespread than that of the so-called striated or voluntary muscular system.

The most significant aspect of these revelations, from the morphological point of view, is that they laid bare this ancestral unstriated muscular system which is equally distributed in the tissues derived directly from the ectoderm

and endoderm. Now the endodermal portion of this musculature is very obvious, because of its activity in all vital phenomena of digestion, circulation, excretion and generation. The application of the term "visceral" to this *endodermal* musculature has both a descriptive and a morphological value. But the extension of the term (as has been common in some quarters) to embrace the whole of the vegetative (sympathetic) nervous system has had the unfortunate effect of causing the somewhat less obvious ectodermally-arising unstriated musculature to be frequently under-valued and sometimes even entirely neglected in morphological terminology. Yet, this *ectodermal* musculature comprises the pilo-motor, glandular and vaso-motor mechanisms of the general body surface and such specialisations as the ciliary and Müllerian muscles in the eyeball region. It is found in all Vertebrata; but most essential of all, it is supplied along with the endodermal musculature by the vegetative nervous system, forming with it, as has been stated, a physiological unity.

The ectodermal musculature arises *in situ* directly from the ectodermal tissues, and the endodermal from the endoderm. This is known (cf. W. H. Lewis, 1910; Brachet, 1921) by actual observation and must follow from phylogenetic considerations if we may trust the work of Darwin and Huxley. The ectoderm and endoderm of Metazoa are homologous layers, or else embryology has gone astray since the time of Pander.

Now the analogies existing between the peristalsis of the gut in Mammalia and the reactions of the "diffuse nerve-net" system of Invertebrata have been admitted by the physiologists, but the homologies of the underlying anatomical mechanisms have not been recognised by morphologists. So far as the homologies of the layers go, the homologies of these derivatives must follow. Consequently, the "endodermal-ectodermal" (or more simply, "*dermal*") system of unstriated musculature in creatures with a segmented mesoderm is homologous with the entire musculature of Coelenterata, Echinodermata, Platyhelminthes and of Mollusca—in brief, of all forms with unsegmented mesoderm. Characterised by undulatory contraction of slow velocity of propagation, long reaction time and low rate of metabolism (however modified this may be in forms with higher specialisations than those of Coelenterata), this muscular apparatus is well adapted for the mechanical propulsion of fluids within tubular cavities (peristalsis), but ill-adapted to respond to the demands for progression upon land (e.g. flat worms, slugs); although a fairly high degree of facility may be achieved in a fluid medium (e.g. octopus and squid families) in the presence of the specialisation of certain organs of higher sense (e.g. eyes).

The *mesodermal* (somatic) musculature is characteristic of all animals with a segmented mesoderm (Annelida, Arthropoda and Chordata) and of these only. When present, this musculature represents an addition to, and not a replacement of, the *dermal* (endodermal-ectodermal) musculature. It is consequently not found so widely distributed in nature; and as contrasted with the diffuse "dermal" musculature, the "mesodermal" is bilaterally segmented

and adapted primarily to one end only—that of propulsion of the body as a whole. It is a system characterised by great velocity of propagation of the wave of contraction, swift reaction time and high rate of metabolism, which has been elaborated for a particular locomotive (animal) want and not for the distribution of nutriment (vegetative) to the tissues.

This antithesis, already inherent in the neurological nomenclature of Meckel (1811) (Das Cerebralsystem mit dem sympathischen oder das animalische mit dem vegetativen), was rendered serviceable to myology by the terms "voluntary" and "involuntary." The discovery that voluntary muscle so-called was "striated" and that involuntary muscle was "smooth," seemed to afford evidence that the physiological antithesis was reflected in the microscopical structure of the tissue.

This division of the musculature upon the basis of its histological structure, valuable as it is, is rendered inadequate by the fact that striation is evident in cardiac musculature and in other "involuntary" musculature such as that of the salamander's mesentery (Schaper) and the muscles that close the shell in certain molluscs (Dahlgren and Kepner). In short, as the latter authors remark, "striation is evidently a feature that belongs to no particular set of muscle cells but may appear in any of them."

To the terms "voluntary" and "involuntary" there are just as cogent objections. A vast number of the actions of the striated skeletal muscles are involuntary reflex actions. Further, as Langley (1921) says, "the fundamental drawback to the use of the word 'involuntary' is that it makes subjective sensations the criterion of classification. It is inappropriate in a science based on objective observation."

But Langley's own substitute "autonomic" is scarcely more happy; for not only does the word "autonomic"—as he himself has confessed (*loc. cit.*)—"suggest a much greater degree of independence of the central nervous system than in fact exists, except perhaps in that part which is in the walls of the alimentary canal," but the word "autonomic" is hopelessly inadequate to describe the musculature of the nervous system of the molluscs and certain worms where the whole neural or "*receptor-expressor*" apparatus is "dermal" in type. (*Vide* Dart and Shellshear, 1922.)

Meanwhile, in a question of nomenclature, we must not overlook Gaskell's confusion. We have considered the unfortunate application of the term "visceral" to a portion of the "striated" (mesodermal) musculature. But the same term "visceral" was also used to apply to the "involuntary" system as a whole and so came to be applicable equally to the "ectodermal" musculature. Now, however tolerant embryology may be toward the designation of endodermally-arising musculature as "visceral," only violence to the meaning of the word can follow its application to the "ectodermal" musculature.

For these reasons the term "*dermal*" has been suggested to apply to the "ectodermal-endodermal" system, as a whole. The term "dermal" has already

been applied by Gaskell to some of the strictly endodermally-arising muscles. It would be of great value to give to this general term "dermal" its complete significance—by including both all the ectodermal and all the endodermal derivatives—not merely to contrast morphologically with the term "mesodermal," but also, emancipating ourselves from subjectivity altogether, to provide for the physiologist and anatomist a rational embryological basis in myological and neurological nomenclature. Thus:

MUSCLE	DERMAL (unstriped)	ECTODERMAL ENDODERMAL
	MESODERMAL (striped)	DORSAL (EXTENSOR) VENTRAL (FLEXOR)

The Term "Visceral" in the Nervous System

If these ontogenetic and phylogenetic facts concerning the bony and muscular tissues are appreciated, their application to the study of the nervous system as a whole is apparent immediately.

The unstriated musculature has been recognised as a physiological unity by virtue of its innervation by the ancestral "nerve-net" (or vegetative nervous system) in both segmented and unsegmented animals. We find in addition, in creatures with segmented mesoderm, a characteristically specialised nervous apparatus for the supply of the segmented musculature. This nervous apparatus forms a second unity of entirely different character, for it is always essentially segmented and bilaterally symmetrical. It is a nervous system characterised by the neurone of Waldeyer, by synapses, and by fixed segmental paths with their well-defined reflex arcs and "invariability of response." In short, it is the elaboration of this segmental anatomical system of skeletal parts, muscles and nerves coincidentally in phylogeny which provides a physical basis for the functional complex known to the physiologist as "voluntary." These form his "voluntary" systems.

I urged this view in putting forward "a new interpretation of the morphology of the nervous system" on behalf of Dr Shellshear and myself at the Philadelphia (1921) meeting of the American Anatomists. At the same meeting Kuntz demonstrated the presence of sympathetic elements developed in the chick after "destruction of the *neural crests and the dorsal portions* of the neural tube," to prove the origin of sympathetic neurones from the ventral lamina of the neural tube. In the same year, Erik Müller and Sven Ingvar published the results of experiments upon Amphibian embryos in which they discovered that the removal of the *ventral half* of the neural tube does not interfere with the production of sympathetic elements. By these ingeniously designed experiments, a beautiful corroboration is afforded of the view enunciated by Weber (1851) that the sympathetic system develops *independently of the neural tube altogether.*

It is evident that the facts afford no substantiation whatever of the conception that the sympathetic system is derived from the neural tube, but

rather present the evidence necessary to show that the vegetative nervous system is the fundamental mechanism upon which the segmented system is later superimposed.

The "additional" or "superimposed" character of the voluntary (or segmented) system has been strikingly demonstrated in the work of Agduhr and Boeke (*vide* J. T. Wilson, 1921) for it has been shown that striated muscle, even in mammals, receives a double innervation. Various views have been put forward by physiologists concerning the significance of this phenomenon, but to the morphologist the universal occurrence of the sympathetic innervation in the body and the limitation of voluntary innervation (and then only in conjunction with a sympathetic innervation) demonstrate beyond all possible doubt the validity of the conception urged here.

Now, Gaskell recognised the presence of segmentation, but believing in the "outgrowth" doctrine of the origin of the vegetative system he imagined that the "visceral" system was an equally segmented system. He overlooked the fact that any segmentation, arising within the ancestrally unsegmented, reticular, vegetative nervous system, was *secondary to* the "neural tube—mesodermal" segmentation. In consequence, he postulated a segmentation for his "visceral" system, coincident with the "somatic" segmentation and represented with the latter in the constitution of the segmented neural tube. According to this postulate, we should find in addition to so-called "somatic" motor and sensory elements, certain "visceral" motor and sensory specialisations within each neural tube segment.

Gaskell applied the theoretical conclusions deduced from his (and Schneider's) study of the musculature to the motor nuclei of cranial nerves, where the bilateral double-column arrangement of these nuclei seemed to lend colour to his classification. The splitting of the "motor column" of nuclei, however, corresponds with certain modifications that have taken place, not in the *gut musculature* itself but in the *segmented mesoderm* which secondarily becomes associated with the gut. However intimately associated with the gut the musculature has become and to whatever degree it has abrogated its original condition to comply with "rhythmical" demands necessitated by the development of increasingly complicated movements of mastication, deglutition and respiration within the animal series, it is recognisable as a "mesodermal" (somatic) musculature of true segmental type. Morphologically speaking, it has nothing whatever to do with the "dermal" system of musculature and only secondarily becomes very intimately correlated with it for obvious economic reasons.

But if confirmation of the "mesodermal" (somatic) character of this musculature were needed, what could possibly be more convincing than the histological investigations of Malone (1913). Even in the most advanced mammalian types the unmistakable "somatic" cellular arrangements are discoverable. No chapter in neurological histology is more clear than this. The cells are typical large *somatic* motor cells, with their characteristic Nissl

substance, the axons are thick and *coarsely medullated*, the nerve-endings are *somatic* in type and the muscle is *striated*. We do not call the motor nucleus of the phrenic nerve "visceral" because the diaphragm moves involuntarily and even rhythmically, nor again the motor nuclei of the V, VII, IX, X or XI cranial nerves which go to mesodermal musculature, whether they respond voluntarily or involuntarily to given stimuli. For theoretical reasons the III, IV, VI and XII nuclei escaped this "visceral" fate at Gaskell's hands, although the XIIth nerve is concerned with the "visceral" function of swallowing food material and supplies "branchial arch" musculature and the others are in segmental series with it. In cases of this character an appeal to physiological criteria is invalid because of the contradictory nature of the answers provided, but the evidence of histology, ontogeny and phylogeny are complete and final.

Although the application of the term "visceral" to these nuclei of cranial nerves has been a feature of American (with the important exception of Malone) and Continental (*vide* Kappers, 1921) neurology, this movement was not countenanced by Elliot Smith (Cunningham, 1914). To my knowledge the statements of Elliot Smith and Malone represent the only remonstrance yet raised against the acceptance of Gaskell's system so far as it concerns the innervation of striated musculature, i.e. the motor side.

The removal of these segmental nuclei (the "special visceral efferent" nuclei of American authors) from the "visceral" category reveals the slender basis upon which the "four-columned" theory was raised, despite J. B. Johnston's (1915) claim to have demonstrated the necessary "viscero-motor" and "viscero-sensory" segmental elements even in the spinal cord of Amphioxus. The "afferent" connection of the vegetative nervous system through the vagus with the central nervous system in the medulla oblongata is well known. Other representation of "afferent visceral" elements in the cerebrospinal axis is inadequately demonstrated anatomically and rests, for the most part, on clinical and physiological induction.

In any case, the term "visceral" (afferent or efferent) can have no morphological significance in neurology apart from its limitation to the vegetative innervation of the endodermal lining of the *archenteric tube* and its derivatives. As such it may include presumably "afferent" elements, by means of which the viscera are brought into more or less intimate connection with the central nervous system. But as soon as the "visceral" (endodermal) elements become entangled in description with the "ectodermal" portion of the vegetative nervous system in supposed contradistinction to the so-called "somatic" nervous system, confusion is bound to result, and particularly in considering the "afferent" or sensory side.

Most productive of harmful results is the extension of the "*visceral afferent*" conception to the study of the special sense organs, which arise in the *ectoderm*. It is evident, *prima facie*, that to call any such ectodermal mechanism "visceral" is to indulge in a loose terminology which neglects all embryological considerations. Even in the case of taste, which appears to have endodermally

arising receptors and ganglion cells in all higher forms, it is definitely known that portion of the mechanism is ectodermal—and not "visceral"—in certain fishes.

Even if the contentions concerning the "visceral" character of taste were to be admitted in the present incomplete nature of our information, it is obvious that no such reasoning can be applied to smell. Tretjakoff (1913) put the facts lucidly enough when he stated "Die rezeptorischen Zellen des Olfaktorius sind den somatisch-rezeptorischen Zellen der Haut der Wirbellosen so ähnlich, dass sie für eine visceralsensorische Komponente zu halten kein Grund vorliegt."

Herrick's criterion, "the relation of the sense to selection and digestion of food" is equally inadmissible. With a full appreciation of the underlying physiological principles involved, it would be possible to make out as good a case for the "visceral" character of the musculature and innervation of the diaphragm, the levator ani and the perineal musculature because of their relation to respiration, defaecation and generation.

CONCLUSION

It is therefore reiterated that far from admitting any claim for the "visceral" nature of smell, restraint should be exercised even in the case of taste, which has been spoken of previously (1920) as a "border-land mechanism." There is certainly no justification in morphological considerations either for a "*visceral cortex*" or for the latest form in which we have the conception appearing when Kappers (1921) calls the striatum a "*sympathisches Gebiet.*"

BIBLIOGRAPHY

Baer, C. E. von. *Ueber Entwickelungsgeschichte der Tiere.* 1828, 1837.

Balfour, F. M. *Comparative embryology.* 1885.

Brachet, A. *Traité d'embryologie des Vertébrés.* Paris. 1921.

Dahlgren and Kepner. *Principles of Animal Histology.* New York. 1908.

Dart, Raymond A. "A contribution to the morphology of the corpus striatum." *Jour. of Anat.* vol. LX. Part I. 1920.

Dart, Raymond A. and Shellshear, J. L. "A new interpretation of the morphology of the nervous system." *Anat. Record,* vol. XXI. No. 1, p. 54. 1921.

—— —— "The origin of the motor cells of the anterior cornu." *Jour. of Anat.* vol. LVI. Pt. II. Jan. 1922.

Darwin, Charles. *Origin of species.* 1859.

Elliot Smith, G. "The central nervous system." *Cunningham's Anatomy,* 3rd edition. 1913.

Gaskell, W. H. *The origin of vertebrates.* London. 1908.

Gaupp, E. *Hertwig's Entwickelungslehre.* Bd. III. 3ter T. 1906.

Gegenbaur, C. *Untersuch. z. vergl. Anat. d. Wirbelth.* Hft. 3. "Das Kopfskelett der Selachier u. s. w." Leipzig. 1872.

Hatschek, B. "Die Metamerie des Amphioxus und des Ammocoetes." *Verhandl. d. anat. Ges. Wien.* 1892.

Herrick, C. Judson. "The connections of the vomero-nasal nerve, accessory olfactory bulb and amygdala in Amphibia." *Jour. of Comp. Neur.* vol. XXXIII. No. 3. 1921.

Hertwig, O. and R. *Die Coelomtheorie, Versuch einer Erklärung des mittleren Keimblattes.* Jena. 1881.

HUXLEY, T. H. "On the theory of the vertebrate skull." (The Croonian Lecture, 1858.) *Proc. of Roy. Soc. Lond.* vol. IV. 1859.

JOHNSTON, J. B. "Cranial and spinal ganglia and the viscero-motor roots in Amphioxus." *Biol. Bull.* vol. IX. No. 2. 1915.

KAPPERS, C. U. ARIENS. *Vergleichende Anatomie des Nervensystems.* Abschnitt II. Haarlem. 1921.

KUNTZ, A. "Peripheral migration and distribution of medullary cells in the absence of spinal ganglia and dorsal nerve roots in embryos of the chick." *Anat. Record,* vol. XXI. No. 1, p. 70. 1921.

LANDACRE, F. L. "The fate of the neural crest in the head of urodeles." *Jour. of Comp. Neur.* vol. XXXIII. No. 1. 1921.

LEWIS, W. H. "Muscular System." *Manual of Human Embryology.* Keibel and Mall. 1910.

MALONE, E. "Somatic motor chain of nerve cells." *Anat. Record,* vol. VII. 1913.

MAURER, F. *Hertwig's Entwickelungslehre,* Bd. III. 1ter T. 1906.

MECKEL, J. F. *Beiträge zur vergleichende Anatomie.* Leipzig. Bd. I. 1808; Bd. II. 1811.

MÜLLER, ERIK and INGVAR, SVEN. "Ueber den Ursprung des Sympathicus bei den Amphibien." *Upsala Läkareförenings förhandlingar.* Ny följd. Bd. XXVI. H. 5–6.

PANDER, C. H. *Beiträge z. Entwick. d. Hühnchens im Ei.* Doktordissertation. 1817.

RABL, C. "Ueber die Differenzierung des Mesoderms." *Verh. d. Anat. Ges. Würzburg.* 1888.

RATHKE, H. *Anat.-philos. Untersuch. über d. Kiemenapparat u. d. Zungenbein d. Wirbelth.* Riga u. Dorpat. 1832.

REICHERT, C. *De embryonum arcubus sic dictis branchialibus.* Dis. inaug. ord. med. Berolini. 1836.

—— "Ueber d. Visceralbogen d. Wirbelth. Im algem. u. d. Metamorph. b. d. Vögeln u. Säugethieren." *Müller's Arch.* 1837.

SCHNEIDER, A. *Beiträge zur Anat. und Entwick. d. Wirbelth.* Berlin. 1879.

STONE, L. S. "Experiments on the development of the cranial ganglia and the lateral line sense organs in Amblystoma." *Anat. Record,* vol. XXI. No. 1, p. 85. 1921.

TRETJAKOFF, D. "Die zentralen Sinnesorgane bei Petromyzon." *Arch. f. mikr. Anat.* Bd. 87. 1913.

WEBER, E. H. *Arch. f. Anat. Phys. und wissensch. Medizin.* 1851.

VAN WIJHE. "Ueber die Mesodermsegments des Rumpfes u. d. Entwickelung des Exkretionssystems bei Selachiern." *Arch. f. mikr. Anat.* Bd. XXXIII. 1889.

WILSON, J. T. "The double innervation of striated muscle." *Brain,* vol. XLIV. Pt. II. 1921.

THE CRANIAL ANATOMY OF POLYPTERUS, WITH SPECIAL REFERENCE TO *POLYPTERUS BICHIR*

By EDWARD PHELPS ALLIS, Jr,
Menton, France.

CONTENTS

	PAGE		PAGE
Introduction	189	Latero-sensory Canals	250
Neurocranium	190	Myology	252
Nasal Sac and Nasal Apertures	198	Eye muscles	252
Osteology	199	Muscles innervated by the nervus trigeminus	252
Parieto-dermopterotic	200	Muscles innervated by the nervus facialis	256
Frontal	201	Muscles innervated by the nervi glossopharyngeus and vagus	257
Nasal	202	Longitudinal ventral muscles	259
Accessory nasal	203	Angiology	260
Os terminale	203	Vena jugularis	260
Ethmoid	203	Afferent and efferent arteries	264
Infranasal and infraorbital bones	204	Carotid arteries	266
Spiracular ossicles	205	Trigemino-facialis chamber	268
Supratemporals and Posttemporal	205	Neurology	269
Basi-exoccipital	206	Nervus and lobus olfactorius	269
Aortic canal	209	Nervus terminalis	270
Aortic canal and occipital region in the 75 mm. *Polypterus senegalus*	211	„ opticus	270
Opisthotic	218	„ oculomotorius	270
Postfronto-sphenotic	220	„ trochlearis	271
Parasphenoid	222	„ abducens	271
Sphenoid	226	„ profundus	271
Ectethmoid	230	„ trigeminus	273
Visceral arches	231	„ facialis	279
Basal line	231	„ acusticus	283
Branchial arches	232	„ glossopharyngeus	283
Hyal arch	235	„ lineae lateralis vagi	286
Opercular and cheek bones	238	„ vagus	286
Palatoquadrate	240	Summary	289
Mandible	245	Literature cited	292
Maxillary	248		
Premaxillary	249		

INTRODUCTION

The present work was begun in 1899, on two large specimens of *Polypterus bichir* purchased in Germany, but it was soon found that they would not suffice for the work contemplated. Several large specimens from the material collected by N. R. Harrison in Abyssinia, and said to also be of *Polypterus bichir*, were later sent me by Professor Bashford Dean, of Columbia University, and still later Professor Dean sent me three heads of *Polypterus ornatipinnis* from the collections at the American Museum of Natural History, New York

City. In addition to this adult material I have had four specimens from 29 cm. to 32 cm. in length, which, as they had only 8–12 finlets, were probably of *Polypterus Lapradei* though said to be of *Polypterus bichir*; and three larvae of *Polypterus senegalus*, 73 mm. to 83 mm. in length, kindly sent me by Professor J. Graham Kerr from the material collected by J. S. Budgett in the Gambia. The dissection of the adult specimens was confided to my assistant, Mr Jugiro Nomura, and the drawings used for the accompanying illustrations are all by him. The three larvae were sectioned, and the one series that proved of any value was given to my assistant, Mr John Henry, with instructions to carefully trace the nerves and blood vessels. While waiting, at different times, for additional material the work was necessarily interrupted, other work undertaken in the meantime still further delayed it, and before it was fully completed and controlled both Mr Nomura and Mr Henry died.

The work has thus not been limited to a single species, which is unfortunate, and it has not been carried through to the extent that was intended, this applying particularly to the nervous system. While it has been in progress I have published several works in which certain of the features of the cranial anatomy have been more or less fully described and discussed, and just as the work is ready for publication I have received a copy of the *Zeitschrift für angewandte Anatomie und Konstitutionslehre* in which there is an important article by Dr Charlotte Lehn, published in Berlin in 1918 and describing the neurocranium of a larva of *Polypterus senegalus*, 76 mm. in length. As my descriptions relate largely to the adult, and include the visceral arches, muscles, nerves and blood vessels as well as the neurocranium, the manuscript is sent to press with but little alteration beyond frequent reference to Lehn's work. Many features referred to, and more or less fully described, in my earlier works are here again described, in order to make the work complete.

Neurocranium

The neurocranium of one of the large specimens from Abyssinia, shown in figs. 7–14, has approximately the proportions of that of the 30 cm. specimen of *Polypterus Lapradei* described by Bridge (1888), but is relatively longer, and less tall and wide than that of the small specimen of *Polypterus* (presumably *senegalus*) described by Traquair (1871) and of the 21 cm. specimen (species not given) described by Pollard (1892). Its dorsal surface is formed by the paired parieto-dermopterotics, frontals, nasals, accessory nasals, ossa terminalia, and premaxillaries, by a single median ethmoid, and by a small portion of the postfronto-sphenotic of either side which is exposed along the lateral edge of the posterior portion of the frontal. Its ventral surface is formed by the premaxillaries, the large median parasphenoid, a small portion of the basi-exoccipital that is exposed between the diverging hind ends of the parasphenoid, and by three small portions of the ethmoid cartilage which appear anterior and lateral to the anterior end of the latter bone.

The orbital fossa is long and low, and occupies about two-fifths of the total length of the neurocranium. Its anterior half, only, is occupied by the eyeball, the posterior half lying internal to the postorbital and prespiracular bones and being completely filled by what Pollard calls the pterygoid and temporal divisions of the musculus adductor mandibulae. The external opening of the fossa leads into the part occupied by the eyeball, and is bounded dorsally by the frontal, posteriorly by the postorbital, ventrally by the lachrymal and the latero-sensory component of the maxillary, and anteriorly by the lachrymal and the antorbital process of the premaxillary. The postorbital process lies at a considerable distance posterior to the hind edge of the external opening of the fossa, and the mesial wall of the posterior half of the fossa corresponds, morphologically, to the hind wall of the orbits of Amia and most of the Teleostei; the flattening out and consequent lengthening of this part of the orbit of Polypterus being an important factor in giving to the entire neurocranium its unusual length.

The nasals, accessory nasals, and ossa terminalia can all be readily removed in alcoholic specimens, but the frontals and parieto-dermopterotics could not be removed, intact, in any of my specimens, without injury to the underlying cartilage. The latter bones could, however, when filed very thin, be stripped off the underlying cartilage without injury to it. The ascending processes of the parasphenoid apparently include the proötics, as will be later explained, and this part of each process could not be removed without breakage of the cartilage.

The primordial cranium, or so-called chondrocranium of the adult is almost entirely of cartilage in the otic and ethmoidal regions, but almost entirely of bone in the orbitotemporal and occipital regions. There is, in the orbitotemporal region, a large perforation of the basis cranii, and directly dorsal to it a still larger perforation of the tegmen cranii. The perforation of the basis cranii may be called the basicranial fontanelle, a name already given to it by other authors, but it is apparently the strict homologue of the fontanelle that I have recently (Allis, 1919*b*, p. 228) called, in Amia and the Teleostei, the fenestra ventralis myodomus. It is closed ventrally by the parasphenoid, and will be further considered when describing the sphenoid bone. The perforation of the tegmen cranii is the supracranial fontanelle. It is roofed by the frontals and parieto-dermopterotics, and is closed, in the natural state, by membrane; and in this membrane, at the posterior third or quarter of the length of the fontanelle, and between the hind ends of the vertical plates of the sphenoid, there was, in the one specimen examined in this respect, the small thin round plate of cartilage described by Pollard, perforated by a small hole. In my 75 mm. specimen of *Polypterus senegalus* there is here a complete bridge of cartilage, as there also was in the larvae described by Budgett (1902) and Lehn (1918). On either side of the supracranial fontanelle there is, in the adult, a large supraorbital fontanelle, which perforates the roof of the posterior portion of the orbital fossa. It is closed dorsally by the frontal, and the tem-

poral division of the musculus adductor mandibulae here has its insertion on the ventral surface of that bone. In my 75 mm. specimen, and in that described by Lehn, the cartilage of the chondrocranium is also here perforated, but in Budgett's 30 mm. larva it is shown as simply hollowed out on its ventral surface, but not perforated, the definitive perforation thus apparently being caused by the insertion of the musculus temporalis.

In Budgett's 30 mm. larva the highest point of the median line of the dorsal surface of the chondrocranium lies between the postorbital processes, in Lehn's 76 mm. specimen it lies somewhat posterior to that point, and in my adults still farther posteriorly, at the hind end of the dorsal surface of the chondrocranium; this change in position of this highest point apparently being caused by a gradual thickening of the cartilage from the hind end of the supracranial fontanelle to the hind end of the dorsal surface of the chondrocranium. From this highest point in the adult, the dorsal surface slopes antero-ventrally at a slight angle, the posterior surface sloping postero-ventrally at an angle of about 30° to the horizontal plane. From the hind edge of the dorsal surface a small flat crista occipitalis, which is horizontal instead of vertical in position, projects posteriorly and slightly overhangs the dorsal edge of the posterior surface.

In the otic region, the median portion of the dorsal surface of the chondrocranium is nearly flat, and on either side of this flat portion there is a large, but non-functional temporal groove. Each postero-lateral corner of the flat surface forms the hind end of the mesial bounding edge of the temporal groove of its side, and corresponds exactly, in topographical position, to the epiotic process of Amia and certain of the Teleostei. The temporal groove has a Y-shaped hind end, one limb of this Y running postero-laterally onto the dorsal surface of the postero-lateral portion of the opisthotic, and the other limb running postero-mesially and then postero-ventrally onto the posterior surface of the chondrocranium. The lateral limb of the Y is a slight depression, only, and lies antero-lateral to the posterior semicircular canal, the mesial limb crossing that canal; the two limbs thus corresponding to the two branch depressions described by me (Allis, 1920*a*) at the hind end of the temporal depression on the dorsal surface of the chondrocrania of Lepidosteus and Rana. The slight depression of the lateral limb lodges the postero-lateral corner of the parieto-dermopterotic, that part of that bone enclosing the hind end of the main latero-sensory canal. The depression of the mesial limb lodges a postero-ventral process of the parieto-dermopterotic, and between this limb and the lateral one, the posterior process of the parieto-dermopterotic projects directly posteriorly. The temporal groove, itself, is almost completely filled by a rounded ridge on the ventral surface of the parieto-dermopterotic.

The dorsal end of the sinus utriculus superior lies considerably mesial to the temporal groove, not far from its fellow of the opposite side. The anterior semicircular canal runs antero-laterally from there, lying mesial to the temporal groove and always enclosed in the cartilage of the chondrocranium.

The posterior semicircular canal runs postero-laterally, anterior to the epiotic process, and then beneath and across the base of the mesial limb of the Y-shaped prolongation of the temporal groove, its course there being marked by a low rounded ridge which forms the boundary between the dorsal and posterior surfaces of the chondrocranium, and the canal lying partly in the cartilage of the chondrocranium and partly in the opisthotic bone. The lateral semicircular canal lies in part internal to, and in part ventro-posterior to the articular facet for the hyomandibula, and traverses both the cartilage of the lateral wall of the chondrocranium and the opisthotic bone, its canal in the latter bone lying internal to the descending arm of the posterior semicircular canal and being in part confluent with that canal.

The anterior end of the lateral semicircular canal lies posterior to the curved descending limb of the anterior semicircular canal, and between these two portions of these two canals there is a marked re-entrant angle in the dorso-lateral edge of the chondrocranium. The anterior edge of the spiracular canal lies in the point of this angle, and the ramus oticus lateralis issues on the dorsal surface of the chondrocranium almost directly mesial to it. The angle is thus a fossa spiracularis, and corresponds to that depressed region on the dorso-lateral edge of the chondrocranium of 14 mm. embryos of Lepidosteus to which I have referred (Allis, 1920*a*) as probably lodging the recessus dorsalis spiracularis. This depressed region of the chondrocranium of embryos of Lepidosteus later becomes spanned by cartilage, and so gives rise to the spiracular canal, the lateral edge of this spanning cartilage forming a connection between the primarily independent sphenotic and pterotic ridges. The chondrocranium of Polypterus thus here remains in the stage of development shown in the 14 mm. Lepidosteus, and a spheno-pterotic ridge such as is found in the adults of the Holostei and Teleostei, is never developed, its two component parts persisting as independent ridges; and this is apparently the condition in mammals, the fossa spiracularis of Polypterus corresponding to some portion of the fossa epitympanica of mammals.

The dorsal portion of the posterior surface of the chondrocranium extends from the hind edge of its dorsal surface to the dorsal edge of the foramen magnum, sloping postero-ventrally at an angle of about 30° to the horizontal plane. This part of the posterior surface is, in reality, the dorsal surface of the occipital portion of the chondrocranium, and its lateral edge, which separates it from the lateral surface of the chondrocranium, is formed by a lateral occipital ridge similar to that found in many of the Teleostei, this ridge starting from the base of the posterior process of the opisthotic, and running along the dorsal margin of the foramen vagum to the ventro-posterior portion of the exoccipital part of the basi-exoccipital. Dorso-mesial to this ridge is a ridge which forms the lateral boundary of the postero-mesial prolongation of the temporal groove, and mesial to this latter ridge is another ridge which forms the mesial boundary of the same prolongation, this latter ridge running dorso-anteriorly into the epiotic process. Between this latter ridge and its fellow of

the opposite side the dorsal surface of the chondrocranium is slightly concave. The conditions in Polypterus thus here resemble those in Amia (Allis, 1897), Scomber (Allis, 1903), and the mail-cheeked fishes (Allis, 1909), excepting in that, in all these latter fishes, the lateral bounding ridge of the posterior prolongation of the temporal groove is confluent with the lateral occipital ridge, the two together forming the bounding edge between the posterior and lateral surfaces of the chondrocranium.

On the lateral surface of the postorbital portion of the neurocranium there is a large articular facet for the hyomandibula, the antero-ventral portion of this facet lying on the lateral surface of the chondrocranium, but its dorso-posterior portion on the lateral edge of the parieto-dermopterotic, and hence actually above the chondrocranium. The antero-ventral end of the facet lies external (lateral) to the anterior portion of the lateral semicircular canal, but its posterior portion dorsal to that canal. The dorsal edge of the facet is formed by a sharp curved ridge which, as described in an earlier work (Allis, 1920*a*), lies partly on the cartilage of the chondrocranium but mainly on the lateral edge of the parieto-dermopterotic, the hollow of the curve presented ventro-posteriorly. That part of this ridge that lies on the chondrocranium is continued posteriorly, on that cranium, internal to the parieto-dermopterotic, and is continuous with the lateral edge of the dorsal surface of the opisthotic, the entire ridge thus forming the pterotic portion of the spheno-pterotic ridge of the chondrocranium. Ventral to the posterior portion of the facet for the hyomandibula there is another ridge, which lies wholly on the opisthotic, and ventral to it is the opisthotic ridge, which begins at about the middle of the lateral edge of the postorbital process, immediately dorsal to the definitive foramen faciale, and runs postero-dorsally across the opisthotic to the hind end of the posterior process of that bone. Between these two ridges there is, on the opisthotic, a concave and roughened surface which gives insertion to the musculi adductor hyomandibularis, adductor operculi, and levatores arcuum branchialium. Ventral to the opisthotic ridge there is a groove, the sulcus jugularis, which lodges the vena jugularis after it issues from the definitive foramen faciale; and ventral to this sulcus there is a large bulla acustica. From the bulla acustica a broad but low ridge runs posteriorly and slightly ventrally, ventral to the foramen vagum and parallel to the lateral occipital ridge, and between these two ridges there is a deep groove which lodges the nervus vagus after it issues from its foramen.

In Budgett's 30 mm. larva the dorso-lateral edge of the otic portion of the chondrocranium is formed by a large ridge, which is said to enclose the lateral semicircular canal and is hence a prominentia semicircularis lateralis. It is called by Budgett the pterotic ridge, and the hyomandibula articulates with its lateral surface. In my 75 mm. specimen this prominentia is found in similar position, and the hyomandibula here also articulates with its lateral surface, but a secondary ridge of cartilage forms the dorsal boundary of the surface of articulation, and it is this secondary ridge that forms the dorso-lateral edge

of this part of the chondrocranium, and is, therefore, the pterotic ridge properly so called, the hyomandibula at no place extending dorsal to it. Mesial to this pterotic ridge, the dorsal surface of the prominentia semicircularis lateralis forms a low and rounded ridge which separates the temporal groove into lateral and mesial portions, the mesial portion lodging the main latero-sensory canal. The parieto-dermopterotic extends laterally beyond this part of the prominentia, its lateral edge resting upon the summit of the pterotic ridge and at no place forming part of the articular facet for the hyomandibula, as it does in the adult. Immediately posterior to the facet for the hyomandibula, the prominentia semicircularis lateralis becomes narrower and more rounded in serial transverse sections, and the pterotic ridge on its dorso-lateral corner gradually vanishes. The prominentia still forms the dorsal boundary of the jugular groove, and the anterior edge of the adductor hyomandibularis is now cut in the sections, this muscle being inserted on the prominentia dorsal to the vena jugularis, between that vein and a large lymph space which extends forward internal to the hyomandibula. Proceeding posteriorly in the sections, a ridge develops on the summit of the prominentia, immediately dorsal to the lymph space above mentioned, this ridge lying ventral to the line prolonged of the pterotic ridge and evidently being, notwithstanding that it lies posterior to the facet for the hyomandibula, that marked ridge on the opisthotic of the adult that forms the ventral boundary of the posterior portion of that articular facet; this ridge vanishing, in the 75 mm. specimen, on the dorsal surface of a posteriorly projecting portion of the otic capsule which lodges the vertically descending portion of the posterior semicircular canal. In the adult the hind end of this ridge forms a slight process on the lateral surface of the posterior process of the opisthotic, as seen in the posterior view of the chondrocranium (fig. 14). The dorsal, or supratemporal branch of the nervus glossopharyngeus runs upward across the surface of insertion of the musculus adductor hyomandibularis, there traversing that muscle, and then perforates the ridge just above described, to reach the dorsal surface of the chondrocranium. In the adult, that part of this nerve that, in this embryo, lies along the external surface of the surface of insertion of the adductor hyomandibularis has become entirely enclosed in the opisthotic.

Lehn (1918, p. 365) considers the ridge just above described on the dorsal surface of the prominentia semicircularis lateralis to be the crista parotica, but as the ridge to which Gaupp (1893) first gave that name, in Rana, forms the dorsal edge of the jugular groove, it seems more probable that it is represented in the entire posterior portion of the opisthotic ridge of Polypterus, as already suggested in an earlier work (Allis, 1920*a*, p. 264).

The cranial cavity occupies about two-thirds of the full length of the chondrocranium, extending from the foramen magnum forward between the orbits to a median wall that separates the foramina olfactoria from each other and that is formed by the mesial portions of the articulating anterior ends of the vertical laminae of the sphenoid. In the orbito-temporal and occipital

regions the bounding walls are entirely of bone, but in the auditory region entirely of cartilage excepting where they are perforated by the large openings that lead into the labyrinth recesses, these openings doubtless being closed by membrane though none could be detected in the dissections. The anterior and posterior portions of the floor of the cavity lie in approximately the same horizontal level, and between them, extending from the foramina optica to the postclinoid wall (proötic bridge), is the large pituitary fossa, this fossa lodging the lobi inferiores in its anterior portion, the hypophysis in its middle portion, and the saccus vasculosus, called by Waldschmidt (1887) the glandular portion of the hypophysis, in its posterior portion, beneath the proötic bridge. The floor of the fossa is perforated, its full length, by the basicranial fontanelle, which is closed ventrally by the parasphenoid. At about the middle of the length of the fontanelle there is, on the dorsal surface of the parasphenoid, a slight median hypophysial depression. The sides of the fontanelle are nearly parallel, and are formed, in the adult, by the basal portions of the vertical laminae of the sphenoid, but in the 75 mm. larva by the cartilaginous trabeculae. The cranial cavity is of approximately equal width throughout the auditory and orbito-temporal regions, and the brain extends its full length. Dorsal to the foramen opticum of either side there is a large but slight depression in the lateral wall, this depression marking the position of the fore-brain.

The ventral portion of the labyrinth recess of either side is occupied by a deep fossa which runs postero-laterally and is separated by a slight and rounded transverse ridge into a small anterior and a large posterior portion. The former lodges the sacculus and the latter the lagena, the thin ventral wall of the latter fossa bulging outward and forming the bulla acustica on the external surface of the chondrocranium. Dorsal to the fossa lagenae there is a fossa in the postero-lateral wall of the recess, this fossa lying in the opisthotic, in the hollow of the curve of that portion of the lateral semicircular canal that projects posteriorly into the hollow of the curve of the posterior semicircular canal, as described by Retzius (1881). The dorsal end of the lagena doubtless lies in this fossa, but I could not definitely determine this in my specimens. Dorsal to the anterior portion of this fossa lagenae there is a small depression which doubtless lodges the saccus endolymphaticus. Antero-lateral to the dorsal edge of the fossa sacculi there is a fossa, slightly double, which lodges the recessus utriculi and the ampullae anterior and lateralis, and antero-lateral and postero-lateral to this fossa are the openings, respectively, of the anterior and lateral semicircular canals. Postero-mesial to the dorsal edge of the fossa lagenae there is a small fossa which lodges the ampulla posterior, and dorso-lateral to this is the ventral opening of the posterior semicircular canal. Two little grooves, which diverge anteriorly and posteriorly from near the median line of the roof of the labyrinth recess, lead into the dorsal ends of the canals for the anterior and posterior semicircular canals, and the little fossa that lodges the dorsal end of the saccus endolymphaticus lies ventro-lateral to the posterior one of these two grooves.

The walls of the labyrinth recess are traversed by all three of the semicircular canals, the part so traversed by the anterior canal lying wholly in the cartilage, internal to the postfronto-sphenotic, while the parts traversed by the lateral and posterior canals are in part enclosed in the opisthotic. The nervi facialis, glossopharyngeus, and ophthalmicus superficialis all enter the labyrinth recess before perforating the cartilaginous wall of the cranium. The nervus facialis, having entered the recess, perforates its cartilaginous wall near the mesial end of the ridge between the fossa sacculi and the fossa that lodges the recessus utriculi and the ampullae anterior and lateralis, and passing ventral to the recessus utriculi opens into the jugular canal, which will be described in connection with the parasphenoid. The foramen for the ophthalmicus superficialis lies slightly anterior to the foramen faciale, close against the ridge of cartilage that forms the mesial wall of the anterior portion of the labyrinth recess, and traverses the cartilage ventro-mesial to the ampulla anterior. The canal for the nervus glossopharyngeus begins in the ventral wall of the labyrinth recess mesial to the mesial end of the ridge between the fossa lagenae and the fossa for the ampulla posterior, and running ventral to the latter ampulla issues at the ventro-posterior edge of the bulla acustica.

Retzius did not find a canalis utriculo-saccularis in the adult specimens he examined. In my 75 mm. larva the large sac formed by the sacculus and lagena was connected by a narrow canal with the basal portion of the sinus utriculi superior, the canal opening into the sacculus-lagena on its mesial surface close to the base of the ductus endolymphaticus.

From the above general description it is seen that the cranium of Polypterus is strictly platybasic in type. The cavum cranii differs markedly, in its general lines, from that of Amia and all of the Teleostei I know of excepting only Amiurus and Silurus, and it as markedly resembles that of many of the Selachii. The resemblance is particularly marked with that of Scymnus, as shown by Gegenbaur (1872, fig. 3, Pl. 4), and slightly less so with that of Chlamydoselachus as described by me (Allis, 1914). In both these latter fishes there is, as in Polypterus, a large pituitary fossa which lodges the lobi inferiores and the pituitary body, the anterior end of the fossa being formed by a presphenoid bolster and the posterior end by a postclinoid wall. The nervus opticus perforates the cranial wall dorsal to the presphenoid bolster in Chlamydoselachus, as it does in Polypterus, and but slightly posterior to that bolster in Scymnus. The pituitary foramen perforates the side wall of the fossa in all three fishes, but differs slightly in position in each of them, perforating the side wall near the middle of the length of the fossa in Polypterus, at its hind end in Chlamydoselachus, and apparently perforating the hind wall in Scymnus. The arteria carotis interna perforates the floor of the fossa by a median foramen, in Chlamydoselachus and Scymnus, while in Polypterus it enters the cranial cavity anterior to the fossa, through the foramen opticum, but this is probably not an important difference, for as the artery in Chlamydoselachus and Scymnus quite undoubtedly runs forward a certain distance

between the cartilage of the fossa and its lining membrane, it lies morphologically anterior to the fossa. In Chlamydoselachus the brain extends forward nearly to the level of the presphenoid bolster, and in embryos doubtless extended onto the bolster, as it does in the adult Polypterus. In Scymnus there is a large presphenoid shelf, as in Polypterus, but it is not said how far forward the brain extends. The anterior end of the cavum cranii is formed, in all three fishes, by a narrow median column which separates the foramina olfactoria from each other, and in the Selachii this column is said by Sewertzoff (1899) to be formed by the trabeculae fused to form what he has called the rostral stalk. A septum nasi, where found, as in Galeus and Mustelus, lies ventral to that stalk. In Polypterus the septum apparently lies dorsal to the trabeculae. But, however this may be, it is evident that the nasal capsules must lie morphologically dorsal to the trabeculae in all these fishes, for the nervi olfactorii always run outward dorsal to the latter cartilages.

Nasal Sac and Nasal Apertures

In my 75 mm. larva of *Polypterus senegalus*, and also in one adult specimen from Abyssinia, the only ones examined in this respect, the nasal sac is divided into five sectors by five longitudinal septa which radiate outward from the axis of the sac. Waldschmidt (1887) also found but five sectors and septa in the 25 cm. to 30 cm. specimens of *Polypterus bichir* examined by him, as did also J. Müller (1846) in what were probably older specimens of the same fish. Wiedersheim (1906), however, says that there are six sectors and six septa in this fish.

In my 75 mm. larva, one of the five septa is horizontal in position and extends mesially from the horizontal axis of the sac to its periphery, the other septa extending dorso- and ventro-mesially and dorso- and ventro-laterally. The nervus olfactorius lies in the horizontal axis of the sac, but it does not enter the sac in the line of that axis, entering it by passing ventro-antero-laterally across the hind end of that sector of the sac that lies immediately dorsal to the horizontal septum, that sector not extending as far posteriorly as the others. The two mesial sectors both extend forward slightly beyond the other three, and there lie mesial to an open space into which they and the other three sectors all open. The ventral one of the two mesial sectors is prolonged anteriorly beyond this space, and there lies in a slight recess in the nasal cartilage. In the adult this projecting anterior end of this sector becomes somewhat separated from the remainder of the nasal organ and forms the "Nebenriechorgan" said by Waldschmidt to have been described by Wiedersheim in a work I have not been able to consult. It is innervated, as Waldschmidt says, by a simple terminal branch of the nervus olfactorius.

Into the open space, above referred to, that lies lateral to the anterior ends of the two mesial sectors of the nasal sac, the anterior nasal tube opens, the base of the tube projecting a certain distance into the space, and being slit a certain distance upward along its lateral surface. Slightly posterior to this

tube, in the lateral portion of the space into which it opens, the posterior nasal passage begins, and runs posteriorly in a slight depression on the lateral surface of the antorbital process of the premaxillary bone. This depression lies between the lateral edge of the nasal bone above and tube 5 of the infra-orbital latero-sensory canal below, and the nasal passage opens posteriorly in a crescentic and slit-like aperture which lies slightly anterior to the anterior edge of the orbit. The anterior nasal tube was, in certain of my preserved specimens, folded back onto the external wall of this posterior nasal passage, and, pushing in that wall, was half imbedded in the groove that lodges the passage.

In one of my large specimens, the only one examined in this connection, the two nasal passages had the same relations to each other and to the nasal sac that they had in the 75 mm. larva, but in a 30 cm. specimen the two nasal apertures both opened into a space that was partially separated from the nasal chamber by a membranous partition, and that was apparently the "Vorhöhle" of Waldschmidt's (1887) description. A large opening led from this atrial chamber into the nasal chamber, and was incompletely bridged by a process of membrane which projected dorso-posteriorly from its antero-ventral edge and touched, but was not fused with, the opposite edge of the opening. Nothing resembling the arrangement here described by Wald-schmidt was found in either of the three specimens examined.

The nasal epithelium of Polypterus would thus seem to be a special development of the rosette form found in certain of the Teleostei and in Chimæra, and it is usually assumed that it has arisen from that form as a result of a thickening of the sensory epithelium and a concomitant deepening of the nasal sac. The nasal capsule cannot, however, have arisen by the simple deepening of a shallow pit, for the terminal branches of the nervi ophthalmicus and maxillaris trigemini both perforate the wall of that capsule and then run forward between it and the nasal sac to issue through the fenestra nasalis. These terminal branches of these nerves both contain latero-sensory fibres, and hence must necessarily have primarily passed external to the nasal capsule, and a simple deepening of the capsule could not have included them within it. There must then have been a forward growth of the lateral wall of the capsule, and it is possible that a similar growth of the primitive sac and nasal epithelium has also taken place.

Osteology

The bones that form the skull of Polypterus are, as is well known, in part so-called primary ones (ossa substituentia) and in part secondary, or dermal ones (ossa investiantia), and certain of them are apparently the equivalents of two or more bones usually found separate and independent in the Holostei and Teleostei. Whether this is due to the invasion, by one bone, of the territory usually occupied by one or more other bones, or is due to the actual fusion of two or more primarily independent bones, cannot be determined from my

material, for, even in my 75 mm. specimen, there is no positive indication, in any of the bones concerned, of two or more separate centres of ossification. It nevertheless seems proper, in certain cases, to assume the fusion of two bones, and to indicate the two components by the use of a compound term.

Parieto-dermopterotic. This bone was called by both J. Müller (1846) and Traquair (1871) the parietal. Van Wijhe (1882) later called it the squamoso-parietal, because of its assumed formation by the fusion of the squamosal and parietal bones of the Teleostei, and I adopted this term in my work on the latero-sensory canals of this fish. The bone, however, only includes the dermal component of the squamosal of the Teleostei, and as the latter bone is currently called by English authors the pterotic, I shall call the bone of Polypterus the parieto-dermopterotic.

The two parieto-dermopterotics, one on either side of the head, are each somewhat rectangular in shape, and they together form the posterior portion of the flat dorsal surface of the neurocranium, extending from the orbito-temporal to the occipital regions and lying upon the otic portion of the chondrocranium. Each bone articulates, in the median line, with its fellow of the opposite side, and articulates anteriorly either with the frontal of its side, alone, or with both that bone and the postero-mesial corner of the frontal of the opposite side, the sutural line between the frontals not always being in line with the suture between the parieto-dermopterotics. The anterior end of each bone rests upon the dorsal surfaces of the postfronto-sphenotic and the vertical plate of the sphenoid, and between these two bones it roofs the hind end of the supraorbital fontanelle. Mesial to the sphenoid it roofs one half of the hind end of the median supracranial fontanelle.

Along the lateral edge of the anterior portion of the bone there is a depressed region which extends forward slightly onto the hind end of the frontal. The anterior portion of this depression lodges the mesial half of the anterior spiracular ossicle. The posterior portion of the depression is deeper than the anterior portion, and lodges the anterior portion of the dorsal end of the spiracular canal, this part of the depression extending downward across the lateral edge of the bone. Posterior to this there is, on the lateral edge of the bone, a concave depression which forms the dorsal portion of the articular facet for the hyomandibula, the dorsal edge of this depression forming a sharp ridge which runs dorso-posteriorly in a curved line from the ventral edge of the lateral edge of the bone, at about the middle of its length, to the posterior end of its dorsal edge.

The postero-lateral corner of the bone rests upon the dorsal surface of the opisthotic, and from the deeper layers of this part of the bone a stout process, directed posteriorly along the dorso-lateral surface of the trunk muscles, gives insertion to a fascia-like formation related to the muscle fibres of the most anterior segment of the trunk muscles that is seen in dorsal views. This process apparently belongs wholly to the dermopterotic portion of the bone, and corresponds to that posterior process of the pterotic that is found in many of

the Teleostei. In Salmo this process is said by Gaupp (1905, p. 678) to be developed in relation to the primary, and not the dermal component of the pterotic, and, furthermore, in all of the Teleostei it is with what is considered to be the primary component of this bone, and not the dermal one, that the hyomandibula articulates. The process of Polypterus is, nevertheless, certainly not of primary origin, and it has quite certainly been developed, like the corresponding process of Scomber (Allis, 1899, p. 55), in relation to the fibrous tissues to which it gives insertion. From the base of this process of Polypterus, and from the ventral surface of the parieto-dermopterotic immediately mesial to it, another process arises which is directed ventro-posteriorly and slightly mesially and lies in that shallow depression on the posterior surface of the chondrocranium that forms a postero-ventral continuation of the mesial arm of the Y-shaped temporal groove. This depression lies immediately lateral to the epiotic ridge, its lateral half lying upon the dorso-posterior surface of the opisthotic, and its mesial half in part upon the cartilage of the chondrocranium and in part upon the dorsal surface of the single median basi-exoccipital bone. Mesial to this ventro-posterior process of the parieto-dermopterotic, the hind end of that bone projects posteriorly somewhat beyond the hind edge of the dorsal surface of the chondrocranium, and there lies upon the dorsal surface of the trunk muscles. The hind edge of the bone is nearly transverse in position, and is slightly bevelled where it is overlapped externally by the anterior edges of the two mesial ones of the three supratemporal bones of its side.

The pterotic portion of the bone is traversed its full length by the main infraorbital latero-sensory canal, the part of the bone so traversed forming a rounded ridge on the ventral surface of the bone which completely fills the temporal groove on the dorsal surface of the chondrocranium. The bone lodges two sense organs of the canal that traverses it, and a tube of the canal issues through the bone slightly posterior to the middle of its length. Immediately posterior to the opening of this tube there is a slight depression which lodges the middle head-line of pit organs.

Frontal. The frontal lies immediately anterior to the parieto-dermopterotic and is the largest bone on the dorsal surface of the cranium. Its mesial edge is nearly straight, and articulates with the corresponding edge of the frontal of the opposite side. Its anterior edge is deeply cut out by a rounded or angular incisure into which the hind end of the nasal fits, the latter bone overlapping externally the frontal. The frontal thus has pointed antero-mesial and antero-lateral corners. The antero-mesial corner rests upon the hind end of the dorsal surface of the median ethmoid. The antero-lateral corner rests upon the flattened dorsal edge of the antorbital process of the premaxillary. Posterior to the latter process the frontal rests upon a portion of the dorsal edge of the ectethmoid, the surface of contact with the latter bone lying slightly mesial to the lateral edge of the frontal. Mesial to these two surfaces of articulation the frontal rests directly upon the cartilage of the chondrocranium, but between the frontal and the cartilage there is, along the lateral

edge of the chondrocranium and underlying the supraorbital latero-sensory canal, a shallow groove which lodges the nerves that supply the sensory organs of that canal.

Posterior to the antorbital process of the premaxillary, the lateral edge of the frontal runs postero-laterally in a more or less wavy line, about one half of the width of the bone here overhanging the orbit. When the bone reaches the postfronto-sphenotic it rests upon and is firmly bound to the dorsal surface of that bone, the lateral edge of the frontal here turning postero-mesially in a rounded angle. The larger, mesial portion of the dorsal surface of the postfronto-sphenotic is slightly hollowed out to receive the frontal, the remaining, lateral portion of the bone forming a slight ridge along the lateral edge of the frontal. On the lateral edge of this part of the frontal there is a small rounded incisure which gives passage to the double tube infraorbital 10—supraorbital 7 of the latero-sensory system (Allis, 1900*a*). Posterior to this tube the frontal roofs for a short distance the main infraorbital latero-sensory canal, that canal lying in a groove on the dorsal surface of the postfronto-sphenotic. The frontal then overlaps externally the anterior edge of the parieto-dermopterotic, and is itself overlapped externally by the anterior corner of the anterior spiracular ossicle, the latter ossicle lying in a slight depression on the hind end of the frontal and being loosely bound to it by tough dermal tissues. Anterior to this spiracular ossicle the lateral edge of the frontal is in articular contact with the posterior one or two prespiracular ossicles, and anterior to all of the prespiracular ossicles it is in articular contact with the postorbital bone.

Mesial to the postfronto-sphenotic the frontal roofs the large supraorbital fontanelle, then rests upon the dorsal edge of the vertical plate of the sphenoid, and mesial to the latter bone, roofs, with its fellow of the opposite side, the median supracranial fontanelle. Along the line where the frontal rests upon the dorsal edge of the vertical plate of the sphenoid, there is a ridge on its ventral surface, this ridge being Y-shaped at its anterior end. Beneath the hind ends of the frontals, in the membrane that closes the supracranial fontanelle, there is the small, round and thin median plate of cartilage already referred to.

The frontal is traversed, the greater part of its length, by the supraorbital latero-sensory canal, but is not traversed by any part of the main infraorbital canal. It lodges three sense organs of the supraorbital canal, and two of the tubes of that canal issue on the dorsal surface of the bone. Beginning mesial to the posterior one of these two tubes, and extending postero-mesially, there is a short and slight depression on the dorsal surface of the bone, which lodges the anterior head-line of pit organs.

Nasal. The nasal is a somewhat oval bone which lies upon the cartilaginous roof of the nasal capsule. Its posterior end is bluntly pointed and lies in the re-entrant angle in the anterior edge of the frontal, overlapping that bone externally and being firmly bound to it by dermal tissues. Its mesial edge overlaps externally, and rests upon the dorsal surface of the posterior process

of the median ethmoid, and is there in contact with, or closely approaches, the corresponding edge of its fellow of the opposite side. Its lateral edge is free, and lies upon the dorsal surface of the antorbital process of the premaxillary. The anterior edge of the bone is straight, or slightly re-entrant, and articulates with the accessory nasal bone.

The nasal is traversed by the supraorbital latero-sensory canal, and lodges the third sense organ of that line. The third supraorbital tubule traverses a notch in the anterior edge of the bone, the fourth tubule traversing a notch in its latero-posterior edge.

Accessory nasal. This bone is a small and somewhat triangular one, immovably bound to the anterior end of the nasal. Its small anterior end rests upon and is bound to the dorso-posterior end of the ascending process of the premaxillary. Its mesial edge fits into a slight groove on the postero-lateral surface of the thickened anterior portion of the median ethmoid, and lateral to the latter bone it rests directly upon the cartilaginous roof of the nasal capsule. Its lateral edge is in contact with the movable os terminale of Traquair's descriptions. The bone is traversed by the supraorbital latero-sensory canal, and lodges the second sense organ of that line. The external surface of the bone lies deeper than the corresponding surface of the nasal, and has not the rugous markings of the latter bone. On one side of the head of the two specimens examined it was found in two pieces.

Os terminale. This bone is a small, curved, somewhat comma-shaped bone traversed by the supraorbital latero-sensory canal and lodging the first sense organ of that line. It is a movable bone, lies in the tough dermis along the postero-mesial edge of the base of the nasal tube, and overhangs the dorsal edge of the fenestra nasalis. It lies along the lateral edge of the accessory nasal, its antero-mesial end resting upon, or adjoining, the dorsal end of the ascending process of the premaxillary. Like the accessory nasal it lies deep in the dermis, and has not the rugous markings of the nasal.

The nasal, accessory nasal and os terminale, together, quite certainly represent the single nasal bone of Amia, as fully explained in my work on the latero-sensory canals of this fish (Allis, 1900*a*).

Ethmoid. The ethmoid is a median bone and is included by Traquair among the primary ossifications. It is said by him to be "a median ossification in the front of the septum narium," and to send "backwards beneath the nasal bones a flat narrow process which is ossified in the membrane superficial to the cartilage." Pollard (1892, p. 400), without making reference to Traquair, says that, "There is no ossification of the cartilage in front of the nasal septum." In all my specimens, from the 75 mm. larva to the largest adult, the bone is strictly a dermal one, lying everywhere external to the cartilage and separated from it by a layer of connective tissue.

The bone has a thickened anterior end and a thinner, plate-like posterior portion, and lies on the dorsal surface of the chondrocranium, in a median depression between the nasal capsules which is much more pronounced beneath

the anterior portion of the bone than beneath its posterior portion. The thickened anterior end of the bone lodges the anterior section of the infra-orbital latero-sensory canal of either side of the head, the two canals anastomosing with each other in this bone, in the median line, but without leaving the slightest indication, even in the 75 mm. larva, of a median tube where the anastomosis has taken place. The bone lodges two sense organs, one belonging to either canal, and the thickened portion of the bone that is traversed by this so-formed cross-commissural canal lies in a groove that has a curved course, convex posteriorly, and crosses transversely the dorsal surface of the rostral process of the chondrocranium immediately anterior to the fenestrae nasales. The rostral process of my adult specimens projects forward slightly beyond the anterior edge of the ethmoid and abuts against the slightly concave posterior surfaces of the premaxillaries. The ethmoid is accordingly not exposed on the ventral surface of the chondrocranium, between the premaxillaries, as Traquair says that it was in his specimen.

Each half of the anterior edge of the ethmoid abuts against and is firmly bound to the premaxillary of its side, and immediately lateral to this surface of contact, the short ascending process of the premaxillary projects postero-mesially in a groove on the lateral surface of the ethmoid, the latter bone thus being held between the two premaxillaries. The ascending process of the premaxillary does not extend the full length of the groove on the lateral surface of the ethmoid, the groove posterior to that process lodging the lateral edge of the accessory nasal, the anterior end of the latter bone resting upon the dorso-posterior end of the ascending process of the premaxillary. The frontal and nasal of either side both overlap externally the hind end of the ethmoid, this being the relations that these bones have to the ethmoid in the Characinidae and Cyprinidae (Sagemehl, 1884 and 1891), but the reverse of the relations that the frontals have to the supra-ethmoid of Parker's (1873) descriptions of *Salmo salar*.

The ethmoid of Polypterus thus corresponds to that middle portion of the dermal ethmoid of Amia that lodges the anterior sense organ of the main infraorbital canal of either side. The lateral portions of the bone of Amia, each of which lodges a second sense organ of the related infraorbital canal, have each fused, in Polypterus, with the premaxillary of its side, as fully explained in my work on the premaxillary and maxillary bones of this fish (Allis, 1900*b*).

Infranasal and infraorbital bones. These bones are usually all described as the infraorbital chain, but the anterior ones are definitely preorbital and infranasal in position and not infraorbital, and they are developed in relation to a definitely preorbital part of the main infraorbital latero-sensory line. The infranasal bones, which correspond to the lateral portion of the median ethmoid and the antorbital bone of Amia, have both fused with the premaxillary, and the infraorbital bones, excepting the anterior and posterior ones, have fused with the maxillary (Allis, 1900*b*).

The anterior infraorbital bone corresponds to the lachrymal of Amia, but is called by Traquair the anterior suborbital. It is a triangular bone the base of which is directed anteriorly and abuts in large part against the hind edge of the antorbital process of the premaxillary, but partly also against the lateral border of the anterior edge of the ectethmoid. Its dorsal edge forms the antero-ventral margin of the orbit. Its ventral edge rests upon the dorsal edge of the maxillary. It is traversed by the main infraorbital latero-sensory canal and lodges one sense organ of that canal.

The next two bones of the chain are suborbital ones, each containing a single sensory organ of the line, and they have both completely fused with the maxillary.

The next, or posterior bone of the chain is called by Traquair the posterior suborbital, but as it forms the posterior margin of the orbit it is a postorbital. Its dorsal edge is in contact with the lateral edges of the frontal and post-fronto-sphenotic, its ventral edge in contact with the dorsal edge of the posterior portion of the maxillary, and its hind edge overlapped externally by the one or two anterior prespiracular ossicles. It is traversed by the main infraorbital canal and lodges one sense organ of that canal.

Spiracular ossicles. In my 49 cm. specimen of *Polypterus bichir* (figs. 5 and 6) there were 7–8 prespiracular ossicles, 2 spiracular ossicles, and 3–5 postspiracular ones, this agreeing approximately with the number of these ossicles shown by J. Müller (1846) in his figure of this fish, and with the number described by Bridge (1888) in that one of his two specimens that had fourteen dorsal finlets. In one of my small specimens, which had 8–12 finlets, there were nine of these ossicles in all, on either side of the head, this agreeing approximately with the number in the specimens described by Traquair, which also had 8–12 finlets, and with the number in that one of two specimens described by Bridge that also had this same number of finlets. This difference in the number of these spiracular ossicles is thus probably a specific character.

Supratemporals and posttemporal. There are three supratemporal bones on either side of the head in all of my specimens, two of them lying in transverse line immediately posterior to the parieto-dermopterotic, and the third one lying posterior to the lateral portion of the lateral one of the other two. The two bones transversely placed are traversed by the supratemporal latero-sensory canal and each lodges one sense organ of that canal, the postero-lateral bone being traversed by the main infraorbital canal and lodging one sense organ of that canal. These three bones, together, thus correspond to the single large supratemporal (extrascapular, Sagemehl) bone of Amia, as fully explained in my work on the latero-sensory canals of this fish.

The posttemporal is a relatively large, plate-like bone in contact anteriorly with the hind edges of the two transversely placed supratemporals, and laterally with the median edges of the postero-lateral supratemporal and the posterior postspiracular ossicle. From the ventral surface of the lateral edge of the bone, at about the middle of its length, a short stout rod-like process

projects antero-ventrally and slightly mesially and gives insertion to a stout ligament which has its origin on the posterior process of the opisthotic. From the base of this process of the posttemporal a slight ridge runs postero-mesially across the ventral surface of the bone, and on reaching its mesial edge turns posteriorly and becomes a stout posterior process which gives insertion to a large fascia-like tendon related to the muscle fibres of that segment of the trunk muscles that is the third one seen in dorsal view of the adult.

Basi-exoccipital. The basi-exoccipital, the occipital bone of earlier descriptions, is, as Traquair has stated, formed by the fusion of the median basioccipital and the two exoccipitals of the Holostei and Teleostei. It has exposed dorsal, ventral, lateral, posterior, and cerebral surfaces. Anteriorly it is everywhere bounded by cartilage. Its dorsal and lateral surfaces are separated from each other by the lateral occipital ridge, already described, this ridge lying wholly on the exoccipital portion of the bone. Its lateral and ventral surfaces are separated by a rounded edge which starts posteriorly on the lateral edge of the vertebra-like hind end of the bone and, lying wholly on the basioccipital portion of the bone, runs anteriorly and slightly ventrally to its anterior end. This edge of the bone is not exposed in the prepared cranium, being covered, throughout its entire length, by the lateral edge of the parasphenoid.

The posterior surface of the bone is formed by the hind end of its basi-occipital portion and the hind edges of its exoccipital portions. The hind end of the basioccipital portion is oval in shape, the vertical axis of the oval being slightly less than half as long as its horizontal axis. It is slightly concave, and gives articulation to the first free vertebra. The hind edges of the exoccipital portions of the bone form the lateral and dorsal boundaries of the foramen magnum, and are bound by membrane to the anterior edges of the occipital vertebral arch.

The lateral surface of the bone, formed largely by its exoccipital portion, is about twice as tall at its anterior as at its posterior end. Its anterior edge is deeply notched, at about the middle of its height, to form the posterior border of the foramen vagum, and from this foramen a deep groove runs postero-ventrally and gradually vanishes toward the hind edge of the lateral surface of the bone. The dorsal edge of this groove is formed by the lateral occipital ridge, its ventral edge by the ridge, already described, that runs posteriorly from the bulla acustica. Both dorsal and ventral to the foramen vagum the anterior edge of the bone is overlapped externally by, and articulates with, projecting processes of the opisthotic, these processes extending posteriorly along the external surfaces of the anterior ends of the lateral occipital and subvagus ridges.

Posterior to and in line with the foramen vagum there are two foramina, one of which transmits, as Lehn has stated, the posterior occipital nerve (z^v) of Fürbringer's (1897) descriptions and the other the ventral root of his anterior occipito-spinal nerve (a^v); the internal openings of these two foramina lying considerably anterior to their external openings. The external opening of the

anterior one of the two foramina lies in the vagus groove on both sides of the head of the one specimen examined, the posterior foramen lying at the dorsal edge of that groove on one side of the head, but, on the other side, definitively on the lateral occipital ridge. A slight groove runs postero-ventrally from each foramen, and ends, postero-ventrally, either in a slight depression, in a relatively deep pit, or in a short canal leading into the bone. Each groove lodges the related nerve for a short distance after it issues from its foramen, the pit, or canal, at its hind end apparently giving passage to an artery, as explained below. Dorsal to and slightly anterior to the posterior one of these two foramina, and dorso-mesial to the lateral occipital ridge, there is a small foramen for the dorsal root of the anterior occipito-spinal nerve (a^d), the internal opening of this foramen lying considerably posterior to the internal opening of the foramen for the ventral root of the same nerve.

The two ventral occipital foramina above described thus correspond almost exactly, in general position, to the foramina for the first and second occipital nerves of my descriptions of Amia, and as the nerves that issue through these foramina in Amia are called by Fürbringer the nerves *z* and *a*, as are also the corresponding nerves in Lepidosteus, the two nerves and their foramina in these three fishes are, in all probability, homologous. The foramina in these fishes are, however, apparently not the homologues of the occipital foramina of Scomber (Allis, 1903) and the mail-cheeked fishes (Allis, 1909), for the foramina in these latter fishes all lie either directly on the lateral occipital ridge, or definitely dorso-posterior to that ridge, this being in accord with Fürbringer's conclusion that the nerve that issues through the anterior one of the foramina in these fishes is the second occipito-spinal one (nerve *b*), and hence the nerve next posterior to the one that issues through the posterior foramen in Polypterus and Amia.

Antero-ventral to the anterior occipital foramen, between it and the transverse plane of the foramen vagum, there is on each side of the head what appears like a simple imperfection in the bone, but a bristle can be pushed into it for a considerable distance. This canal lies in the line prolonged of the two little pits, or canals, at the hind ends of the two grooves that lead postero-ventrally from the two occipital foramina, and in the adult nothing could be found entering either of them. In the 75 mm. larva a branch of an intervertebral artery penetrated the bone in a position corresponding to that of each of the two posterior canals, but nothing was found entering the bone in the position of the anterior canal. The two intervertebral arteries here concerned arose as a single artery from the dorsal aorta immediately after that artery issued from the hind end of the aortic canal, each artery first sending a branch into the canal in the basioccipital, then one into the cranial cavity through the foramen for the related occipital nerve, and then continuing onward, doubtless in relation to a muscle septum, but this was not traced. From the posterior one of these two intervertebral arteries, previous to the branch sent into the cranial cavity, a branch was sent posteriorly, and from this branch a branch

was sent into the cranial cavity through that foramen in the occipital neural arch that gives passage to the ventral root of the related spinal nerve (nerve b^v). No separate artery arising directly from the aorta was found in relation to this neural arch, but one was found in relation to the first, third and fourth free vertebrae. Between the arteries sent to the first and third vertebrae an artery arose from the dorsal aorta, but it was apparently not distributed to the segment of the second vertebra, this vertebra being supplied by a posterior branch from the artery to the first vertebra.

The dorsal surface of the basi-exoccipital forms the ventral portion of the gently sloping posterior surface of the chondrocranium. For a short distance immediately anterior to the foramen magnum, the mid-dorsal line of this surface is nearly horizontal in position, the bone here forming an arch above the medulla. Anterior to this short horizontal portion the surface widens gradually and slopes gently upward to the anterior edge of the bone. The two epiotic ridges, one on either side, are prolonged slightly onto the basi-exoccipital, and separate the exposed portion of its dorsal surface into three regions, one median and two lateral, each of which is slightly concave and is prolonged dorso-anteriorly in a corresponding depression on the cartilaginous portion of the posterior surface of the chondrocranium. Each lateral depression forms the mesial portion of that shallow depression on the posterior surface of the cranium that forms the ventro-mesial arm of the Y-shaped temporal groove and lodges the ventro-posterior process of the parieto-dermosphenotic. The median depression is apparently formed by what Lehn (1918, p. 360) calls the supratemporal grooves, but as the depression ends dorso-anteriorly at the hind edges of the parieto-dermosphenotics it corresponds to the postero-ventral prolongations of the supratemporal grooves of my descriptions of Scomber (Allis, 1903) and not to those grooves themselves, the grooves lying on the dorsal surface of the cranium.

The hind edges of the exoccipital portions of the basi-exoccipital form the lateral and dorsal boundaries of the foramen magnum, the lateral edges of the foramen inclining upward and forward. The basioccipital portion of the bone projects posteriorly, beyond its exoccipital portions, a distance equal to about one half the thickness of the first free vertebra, and its dorsal surface is here slightly concave, transversely, on either side of the median line. In these concavities the rounded bases of a pair of free dorsal neural arches rest, the anterior edges of the arches resting against and being connected by membrane with the hind edges of the exoccipital portions of the basi-exoccipital. These two arches, one on either side, are fused with each other in the median line dorsal to the spinal cord, and a short dorsal neural spine articulates with, and is firmly bound to, the dorsal portions of their posterior edges. The neural arch of either side is perforated by the ventral root of a spinal nerve, and either perforated, or notched on its anterior edge, by the dorsal root of the same nerve. The next posterior, or second pair of dorsal neural arches are fused with the first free vertebral centrum, the arch of either side being perforated

by both roots of the related spinal nerve. The first neural arch is accordingly an occipital arch, related to a vertebral centrum that has fused with the basi-exoccipital, and the nerve that perforates it is actually the posterior occipital nerve. It is however called by Fürbringer (1897) the second spinal nerve.

The rounded edge that separates the lateral and ventral surfaces of the basi-exoccipital, and the larger portion of the ventral surface of that bone, are covered externally by the hind end of the parasphenoid, the two bones being so firmly anchylosed that they could not be separated without breakage even in an alcoholic specimen that had been long macerated. In a fresh specimen they could probably be separated, for the two bones are wholly separate and distinct in my 75 mm. larva. In the hind edge of the parasphenoid there is a large and deep V-shaped incisure, which extends about one half the length of the basi-exoccipital, and a corresponding portion of the ventral surface of the basi-exoccipital is exposed between the limbs of the V. In the middle line of this exposed surface there is a large foramen which leads into the aortic canal, and on either side of this foramen there is a round depression which lies partly on the basi-exoccipital and partly on the parasphenoid and gives origin to a stout ligament which runs almost directly laterally and is inserted on the shoulder girdle.

Aortic canal. The aortic canal of Polypterus was, so far as I know, first particularly described by Bridge (1888), and he refers to it, in the plural, as the basicranial canals. Of these canals he says: "In both specimens the somewhat massive bone occupying the basioccipital region and continuously surrounding the foramen magnum, and possibly including also the centrum of the first vertebra, is perforated near the posterior end of its under surface, at the extremity of the parasphenoid, by a small median foramen. Traced forwards this foramen leads into two divergent canals, which at first lie between the basioccipital above and the parasphenoid below, but more anteriorly, between the last mentioned bone and the cartilaginous basis cranii. Finally, after perforating the roots of the lateral wings of the parasphenoid, the canals open into the orbit near the postero-inferior angles of the lateral plates of the sphenethmoid, and below the notch for the second and third divisions of the fifth nerve. The median foramen apparently transmits the dorsal aorta, and it is probable that the divergent canals are traversed by either the internal or external carotids, or possibly by both arteries during a portion of their course. Although the eye muscles in Polypterus are not in any way related to these canals, it is by no means improbable that the latter represent the orbital canals so characteristic of many Teleostean fishes."

Pollard (1892) says of this canal: "The dorsal aorta runs both forwards and backwards. The precardiac portion penetrates immediately into the skull passing into the body of the last vertebra which takes part in the formation of the cranium. Further forwards it lies between the cranium and the parasphenoid dividing and passing out with each wing of the latter to join the efferent 1st branchial. The common trunk thus formed runs on as the oph-

thalmic artery on each side." In one of his figures (fig. 12, Pl. 28) he shows the canal lying between the basi-exoccipital and the parasphenoid, while in another (fig. 23, Pl. 28) he shows it wholly enclosed in the basi-exoccipital.

Budgett (1902) does not particularly describe this canal in his 30 mm. larva of *Polypterus senegalus*, but he describes a so-called subaortic bridge of cartilage which projects ventrally beneath the hind ends of the parachordals and encloses a short section of the aorta. Of this bridge he says: "The basi-occipital region does not completely envelope the anterior end of the notochord, but is composed of two halves (the parachordal cartilages) abutting on two sides of the front end of this structure. Posteriorly these two masses of cartilage send wings ventrally which meet and fuse beneath the dorsal aorta, enclosing it in a short canal which is roofed in by the notochord itself. Anteriorly to the bifurcation of the aorta, the basioccipital cartilages fuse below the notochord, sending forward a narrow medial plate of cartilage which underlies the tip of the notochord."

In a figure giving a lateral view of the occipital portion of a reconstructed skull, Budgett (*l.c.* fig. 4, Pl. 33) shows the aorta turning dorso-anteriorly immediately anterior to his subaortic bridge and there being immediately hidden from view by the parachordal cartilage, and as the parachordals are said, in the quotation just above given, to be here separated from each other by the anterior end of the notochord, it would seem as if the aorta must lie in a deep groove on the ventral surface of the basal plate. The descriptions and figures are, however, not in accord as to this, and it would furthermore seem as if there must be some error either in the figures or in the descriptions of them. In the fig. 4 above referred to, the subaortic bridge is shown lying considerably posterior to the hind end of the otic capsule, and, anterior to the bridge, the parachordals run dorso-anteriorly at a considerable angle to the ventral surface of the notochord. Fig. 1 on the same plate is said to give a lateral view of the same reconstructed primordial cranium with the ex-occipital region cut off, and figs. 2 and 3 to give posterior and anterior views of the same. The subaortic bridge of fig. 4 should accordingly be excluded from figs. 1, 2 and 3. The aorta is however shown, in each of these three figures, enclosed within an arch of cartilage, and in figs. 2 and 3 this arch is said, by index letters, to be the subaortic bridge. It must then be that the aorta is again enclosed in a canal in the parachordal cartilage after it has traversed the canal formed by the bridge at its hind end, but this is in no way indicated in the descriptions. In fig. 4 the notochord is shown decreasing rapidly in size as it approaches the subaortic bridge, but in a cross-section through it, shown in fig. 2, and hence presumably close to the hind end of the otic capsule, the notochord has not diminished in size and is even approximately as tall, in cross-section, as it is in the region of the aortic bridge.

In the adult Polypterus, I find the aortic canal penetrating the ventral surface of the basioccipital immediately anterior to its vertebra-like hind end, between the diverging hind ends of the parasphenoid. The canal then turns

forward and, wholly enclosed in the basioccipital, extends to the anterior end of that bone. There it bifurcates, the bifurcations passing outward, on either side, in the cartilage of the basis cranii and opening in the canal enclosed between the lateral, ventral and mesial plates of the lateral wings of the parasphenoid. The cartilage in which these bifurcations lie extends the full length of the basal portion of the labyrinth region, and separates the anterior end of the aortic canal from the hind end of the pituitary fossa. This cartilage is thick in the median line, but thinner on either side, and raised portions of the parasphenoid there support the anterior walls of the bifurcations of the aortic canal.

The aortic canal and occipital region in the 75 *mm.* Polypterus senegalus. In my 75 mm. specimen of *Polypterus senegalus* I find no trace of the cartilaginous subaortic bridge of Budgett's descriptions, nor does Lehn describe it in her 76 mm. one. There is, however, on the ventral surface of the basal plate of the chondrocranium, a groove, with ventro-laterally projecting edges, which lodges the dorsal aorta and its diverging branches (the lateral dorsal aortae), and hence is an aortic groove.

The floor of the postpituitary portion of the cavum cerebrale cranii begins anteriorly in a narrow transverse bridge of cartilage which extends from one cranial wall to the other and is the homologue of the cartilago acrochordalis of Sonies's (1907) descriptions of embryos of the chick and duck. It represents, at this age, the proötic bridge of the adult and has concave anterior and posterior edges, the widened base of the bridge forming, on either side, a ridge on the cerebral surface of the lateral wall of the cranium. Anteriorly this ridge vanishes on the cranial wall opposite the line of the cerebral sulcus that lies along the dorsal edge of the lobus inferior. Posteriorly it descends gradually and becomes continuous with the dorsal edge of the thick cartilage that forms the lateral boundary of the posterior portion of the basicranial fontanelle, and this posterior part of the ridge is connected by membrane, throughout its entire extent, with its fellow of the opposite side, this membrane and the cartilaginous proötic bridge forming the roof of the posterior portion of a dorsal, but non-functional myodomic cavity (Allis, 1919*b*) which lodges the large pituitary body. The dorsal portion of the thick cartilage that forms the posterior boundary of the basicranial fontanelle thus forms the posterior boundary of a fenestra basicranialis posterior, the ventral portion of the cartilage forming the posterior boundary of a fenestra ventralis myodomus (Allis, 1919*b*). What Waldschmidt (1887) calls the nervous portion of the hypophysis lies beneath the cartilaginous proötic bridge, the glandular portion lying beneath the membrane posterior to that bridge. Waldschmidt says that this so-called glandular portion of the hypophysis of this fish is in no sense a saccus vasculosus such as is found in the Teleostei, but as the two structures evidently are, as Waldschmidt says, genetically related, it may be called the saccus. The pituitary vein of either side perforates the lateral wall of the myodomic cavity beneath the anterior portion of the proötic bridge and

immediately falls into the infraorbital branch of the vena jugularis. The perforation of the roof of the cavum sacci vasculosi, the fenestra basicranialis posterior above referred to, is described by Lehn (1918, p. 364) in her 76 mm. specimen, but it is not the fenestra basicranialis posterior of her descriptions, which lies posterior to this and will be referred to later.

The basicranial fontanelle ends slightly posterior to the hind end of the saccus vasculosus, and from there as far back as the tip of the notochord, the basal plate is an unbroken plate of cartilage. From that point, posteriorly, to the point of bifurcation of the aortic groove, the basal plate encloses the anterior end of the notochord and is somewhat thickened in the median line, but the cartilage is imperfect in places both dorsal and ventral to the notochord, the parachordal plates of opposite sides not yet having completely fused around it. This thickening of the cartilage here forms a median ridge on the ventral surface of the basal plate, this ridge increasing in height posteriorly and, at the point of bifurcation of the aortic groove, projecting ventrally below the level of the ventral surface of the aorta. The lateral surfaces of the ridge are here scooped out to form grooves which are directed postero-mesially and lodge the lateral dorsal aortae, and when these grooves unite with each other in the median line, the ventral portion of the ridge is pinched off and projects posteriorly as a short process which extends to the point where the lateral dorsal aortae join the median aorta. This little process may be called the median subaortic process. It is not shown or mentioned by Budgett in his descriptions either of his 30 mm. larva or of the older ones examined by him, but is described by Lehn (1918, p. 257) in her 76 mm. specimen. Pollard (1892) shows it in two of the sectional views of his 21 cm. specimen, and of it he says: "In front of the vertebral elements which have been drawn into the base of the skull there occurred in the youngest specimen of Polypterus a small oval block of cartilage curiously surrounded by a thin shell of bone and above it lay the thread-like termination of the notochord." This would seem to mean that Pollard found the projecting hind end of the process of my larva as an independent piece of cartilage, but Winslow (1898), who examined drawings made by Kingsley of Pollard's sections of this same specimen says: "A peculiar rod of cartilage projects a short distance backward from beneath the middle of the basilar plate."

Anterior to the median subaortic process, the lateral aortic groove of either side diverges from the median ridge on the ventral surface of the basal plate, and its mesial boundary is then formed by a sharp cartilaginous ridge which diverges from the median one. The lateral boundary of the groove is here at first formed by an anterior prolongation of the lateral bounding ridge of the median, posterior portion of the aortic groove, but this ridge gradually vanishes on the rounded ventro-mesial edge of the otic capsule, the groove then lying in the angle formed where that capsule is joined by the parachordal plate, and there gradually vanishing anteriorly. Posterior to the subaortic process, the lateral aortic grooves of opposite sides fuse to form a median groove which lies directly

beneath the notochord, the notochord here lying against the ventral surface of the basal plate and projecting ventrally beneath it into the groove. Proceeding posteriorly, the ventrally projecting ridge that forms, on either side, the lateral boundary of the groove gradually diminishes in height, and the parachordal cartilages there recede slightly from the notochord, thus leaving a small fenestration in the parachordal plate which lies approximately in the transverse plane of the anterior edge of the foramen vagum, and hence in that of the hind ends of the otic capsules, and is the fenestra basicranialis posterior of Lehn's descriptions. This fenestra is spanned, at about the middle of its length, by a bridge of membrane bone which encloses the notochord. Posterior to the fenestra the dorsal edge of the mesial edge of each parachordal is in contact with the lateral surface of the notochord, the notochord, enclosed in bone, lying between the parachordals with exposed dorsal and ventral surfaces which form, respectively, the median portion of the floor of this part of the cavum cranii, and the roof of the here shallow aortic groove on the ventral surface of the basal plate.

Up to the point where the lateral aortic canals unite with each other in the median line, there is no indication of ossification in relation to the cartilage that surrounds the notochord, and even in the adult the cartilage still persists in this region. In my sections, which were double stained in Weigert and magdala-red fluids, a superficial layer of the cartilage is everywhere stained a reddish colour which is much deeper in certain regions than in others. This layer contains occasional cells, found singly and somewhat separated from each other, and coloured lines extend inward from it between the cells of the deeper portion of the cartilage, certain of these lines occupying the entire space between adjoining cells, while others are completely surrounded by a less deeply staining matrix which separates the cells. In certain places these lines seem to be fibrous, but in others they are certainly simply a staining of the matrix of the cartilage. Superficial to this layer there is, on the cerebral surface of the cartilage, a thin membranous layer which is in most places closely applied to the cartilage, but in certain places separated from it. This membrane is quite certainly the dura mater, or a part of it, and where it has separated from the cartilage scattered cells are found in the intervening space. On the external surface of the cranium fibrous lines separate, in certain places, from the external surface of the deeply staining superficial layer of the cartilage and are continuous with the perichondrial fibrous tissues that lie external to it. Throughout the notochordal portion of the region there is, internal to and concentric with the superficial reddish layer on the cerebral surface of the cartilage, a second layer of strictly similar appearance, and between the two layers there is a layer of cells which look like the cartilage cells found in places where the cartilage is undergoing resorption. Beginning somewhat anterior to the base of the median subaortic process, the cells in that portion of the cartilage of the basis cranii that lies dorsal (cerebral) to the notochord are encircled, in groups of one or more, by the reddish lines above described, and in the transverse

plane of the tip of the subaortic process these cells all become separated from the remainder of the cartilage by a prolongation of the inner one of the two reddish layers above referred to. A median portion of the cartilage, which lies directly upon the dorsal surface of the notochord and which is concavo-convex in transverse section is thus here incompletely separated from the parachordals, and as the latter cartilages do not here reach the notochord, and as the fenestra basicranialis posterior of Lehn's descriptions begins immediately posterior to the median cartilage, the latter cartilage fills the anterior end of the fenestra and apparently represents a stage in the occlusion of it. This little cartilage is described by Lehn (1918, p. 363) in her specimen, and is there said to be continuous anteriorly with the cartilage of the basis cranii.

In the basioccipital region resorption cavities are forming in the cartilage, and they lie, in certain places, internal to the reddish superficial layer of the cartilage, but in others include that layer. Where perichondrial bone has been formed it occupies exactly the place of this reddish layer, and it is difficult to tell where bone ends and the unossified tissue begins. The tissue thus cannot be cartilage, for perichondrial bone is said never to be formed by direct ossification of cartilage. It is however skeletogenous tissue of some sort, and it lies directly upon the cartilage without a recognisable intervening layer of tissue of any sort, the conditions here thus seeming to be similar to those described by Schauinsland (1906, p. 445) in the neural arches of Amia, where the first-formed bone is said to develop in the perichondrium (im Perichondrium). Nowikoff (1909) says that, in the tibia of the new-born mouse, the first-formed bone develops external to the perichondrium, but Schäfer (1893, p. 275) makes the general statement that true membrane-bone (that is, perichondrial bone), "lies underneath the perichondrium, and closely investing the surface of the cartilage." There is thus difference of opinion as to how this bone develops.

The parasphenoid, in the region of the subaortic process, underlies the cartilage of the basis cranii, separated from it by dense fibrous tissue, and its lateral edges project laterally on either side so as to partly floor the related diverging branch of the aortic groove. Posterior to the point where these diverging branches unite with each other in the median line, and as far back as the point where the lateral dorsal aortae fuse with each other to form the median dorsal aorta, the notochord lies on the ventral surface of the cartilage of the basis cranii, directly dorsal to the median subaortic process. Around the subaortic process a layer of perichondrial bone is forming, and laminae of bone are sent outward from it to the inner surface of the dense fibrous tissue that lies between it and the parasphenoid, this perichondrial bone and the related laminae forming part of the basioccipital. The lateral edges of the parasphenoid here extend upward, on either side, to the cartilaginous lateral edge of the aortic groove and abut directly against that cartilage, with a somewhat broad and flattened edge, the aortic groove of more anterior sections

thus becoming a canal the ventral portions of the walls of which are formed by the parasphenoid. From here the aortic groove extends posteriorly to the hind end of the parachordal cartilage, the cartilaginous lateral edges of the groove projecting ventrally as slight ridges which increase somewhat in height at the hind end of the cartilage.

Posterior to the hind end of the median aortic process, that portion of the basioccipital bone that develops in relation to that process still continues, but it is here a purely membrane bone, developed internal to the dense fibrous tissues in which the parasphenoid is imbedded, and having no relations whatever to the cartilage of the chondrocranium. Farther posteriorly, in the transverse plane of the anterior edge of the foramen vagum, this portion of the basioccipital extends upward on either side, internal to the parasphenoid, until it reaches the cartilage of the basis cranii, where it fuses with the layer of perichondrial bone developed in relation to that cartilage, the dorsal aorta thus here being wholly enclosed in the basioccipital, that part of the bone that forms the roof of the canal being developed in relation to the parachordal cartilages, but the part that forms the floor and lateral walls of the canal being developed in relation to fibrous tissue and in no relation whatever to existing cartilage.

At the hind end of the otic capsule, the parachordal of either side, as seen in transverse sections, is directed dorso-laterally, and immediately posterior to the capsule its dorsal edge forms the ventral boundary of the foramen vagum. From that point it diminishes gradually in height and ends slightly posterior to the foramen for the anterior occipital nerve (the nerve z^v of Fürbringer's descriptions), that foramen lying immediately dorsal to the hind end of the cartilage, in membrane bone that forms part of the exoccipital. Posterior to this the notochord increases rapidly in size, is circular in transverse section, and is completely surrounded by a layer of deeply staining tissue that looks like bone and includes the outer layer of the fibrous portion of the notochordal sheath. From this deeply staining layer, processes of bone of membrane origin project outward along the dorso-lateral and ventro-lateral lines of the notochord. The dorso-lateral processes extend posteriorly to the hind end of the skull, form the posterior portions of the exoccipitals, and end dorsally in connective tissues that here form the roof of the cranial cavity. The ventro-lateral processes are short, and correspond in position to the aortic supports of Budgett's descriptions of the vertebrae in his 90 mm. larva of this fish. They are continuous, at their outer ends, with that portion of the basioccipital, of membrane origin, that forms the lateral and ventral bounding walls of the aortic canal, and this bone is now beginning to break through on its ventral surface preparatory to the exit of the aorta from its canal. This portion of the basioccipital still lies wholly internal to the dense fibrous tissue that separates it from the parasphenoid, the latter bone here being represented only by its two projecting hind ends, one on either side, these ends lying external to thickened portions of the basioccipital that correspond to those slightly

raised and pad-like portions of the bone which, in Amia (Allis, 1897), give support to the parasphenoid. Irregular laminae of membrane bone extend between the dorso-lateral and ventro-lateral processes of either side.

Slightly posterior (7 sections) to the hind ends of the parachordals, cartilage appears within the basal portions of the dorso-lateral bony processes and extends posteriorly through about 25 sections, the bases of these cartilaginous processes resting directly upon the deeply staining outer layer of the notochord and their sides being lined by perichondrial bone which is continuous with that layer, and is prolonged dorsally beyond the cartilaginous processes to form the dorsal portions of the exoccipitals. The ventral roots of the second pair of occipital nerves (nerves a^v, Fürbringer) issue from the cranial cavity immediately dorsal to these cartilaginous processes, there perforating the membrane-bone portions of the exoccipitals, the dorsal roots of these nerves issuing, almost directly dorsal to the ventral roots, across the hind edges of the exoccipitals. These cartilaginous processes are thus evidently the dorso-lateral vertebral processes of a vertebra that has fused with this part of the cranium. They are described by Lehn (1918, p. 351) in her 76 mm. specimen, and are said to be continuous, in a 55 mm. specimen, with the parachordal cartilages anterior to them. The processes are continuous posteriorly, as Lehn has stated, with a thin cartilaginous ring which surrounds the notochord, lying between its deeply staining outer layer and a concentric ring of bone that develops external to it. This thin ring of cartilage would seem to be similar to the one described by Schauinsland (1906, p. 444) in Amia and there called by him the skeletoblastic layer. Immediately posterior to this ring, there is a second pair of dorso-lateral cartilaginous processes, and they form the basal portions of the free occipital arches. Their bases break through the ring of bone concentric with the notochord and rest directly upon its outer, deeply staining layer. The third, and posterior, pair of occipital nerves, the second spinal nerves of Fürbringer's descriptions, perforate the membrane-bone portions of these arches.

Comparing the conditions above described in my 75 mm. larva with those described and figured by Budgett in his 30 mm. one, it is first to be remarked that the notochord, as shown in Budgett's fig. 4, Pl. 33, would seem to end considerably posterior to the otic capsules. Its mid-dorsal line is shown curving rapidly ventrally, and as Budgett says that the notochord tapers "suddenly...anteriorly...towards its termination," one naturally concludes that this tapering is here represented, and that it continues uninterruptedly to the anterior end of the chord. This is however not the case, for Budgett says that the tip of the notochord reaches the hind end of the membrane that closes the "very large fontanelle in the posterior end of which lies the hypophysis." The notochord must accordingly extend forward a considerable distance beyond the point where it is shown, in Budgett's figure, passing between the hind ends of the parachordal cartilages, and it must there run upward and forward at a considerable angle to the vertebral part of the chord. The post-

auditory portions of the parachordals also run dorso-anteriorly at a considerable angle to the auditory portions, thus leaving a marked depression in the mid-dorsal line between the hind ends of the otic capsules and the second neural arch of this larva. No such depression can be noticed in my transverse sections, and it is not shown in the median section of Lehn's specimen (1918, fig. 4).

The subaortic bridge of Budgett's descriptions is shown by him lying immediately posterior to the point where the notochord passes upward between the hind ends of the parachordals, and directly beneath the expanded base of the exoccipital cartilage of his descriptions. The nerve XI of his descriptions, my anterior occipital nerve, issues across the anterior edge of the exoccipital cartilage, the first spinal nerve of his descriptions, my second occipital, issuing across the posterior edge of that cartilage. The subaortic bridge of this 30 mm. larva must then be represented, in my 75 mm. larva, by the little ventrally projecting processes on the extreme hind ends of the parachordal cartilages, and as these little processes do not extend ventrally beyond the level of the dorsal surface of the aorta, the bridge of Budgett's larva must have undergone considerable resorption, the part so resorbed being replaced by membrane bone that forms part of the basioccipital. Anterior to this point, a similar resorption of cartilage, and its replacement by membrane bone, must also have taken place, for at no place does cartilage bound the entire lateral surface of the aorta.

Anterior to the bifurcation of the aorta, the parachordal cartilages of opposite sides are said by Budgett to fuse with each other beneath the notochord, this apparently being represented, in my larva, by the basal portion of the median subaortic process. From this point Budgett says that a narrow median plate of cartilage is sent forward as far as the tip of the notochord. There must then be an open space on either side of this median band, between it and the ventral edge of the otic capsule of its side. No such space exists in my larva, the cartilage of the basis cranii here being complete, and the tip of the notochord lies at a considerable distance (40 sections of 15μ thickness) posterior to the hind edge of the basicranial fontanelle.

The so-called exoccipital cartilage of Budgett's larva is evidently represented, in my larva, by the anterior dorso-lateral vertebral process, for these two cartilages have similar relations of the nerves. In Budgett's larva the so-called first lateral vertebral process is shown by him attached to the base of the exoccipital cartilage, and there is no corresponding so-called ventral vertebral process. The second lateral process of his larva lies postero-ventral to the base of the first free spinal neural arch, and there is a corresponding ventral process. In my larva the first dorsal rib is attached to the second dorso-lateral vertebral process, in relation to which the free occipital arch is developed, and there is no corresponding ventral rib. The second dorsal rib and the first ventral one are both attached to the first free vertebra. The anterior lateral and anterior ventral vertebral processes of Budgett's larva are

accordingly not represented by ribs in my larva, and must either have both disappeared or be represented, one or both, in the large ligament which, in the adult, extends from the ventral surface of the hind end of the basioccipital to the shoulder-girdle. This ligament is well developed in my 75 mm. larva, arising from the lateral surface of that portion of the basioccipital that forms the hind end of the aortic canal and there being continuous with the tough fibrous tissue that lies between the basioccipital and the parasphenoid.

The first free neural arch of Budgett's larva is thus the free occipital arch of the adult, and the related lateral vertebral process must have acquired connection with it by a continuation of the dorsal shifting of these lateral processes that is evident in Budgett's larva. Two vertebral centra and one neural arch have then fused with the hind end of the cranium during the ontogenetic development of this fish. In my 75 mm. larva the wholly enclosed portion of the aortic canal lies anterior to the anterior one of these two vertebrae, the posterior opening of the canal lying ventral to that vertebra and in a nearly horizontal position. In transverse sections through this opening, the processes of the basioccipital closely resemble the haemal processes shown by Budgett in sections through both the anterior and posterior portions of the body of his 90 mm. and 130 mm. specimens of this fish, and the raised, pad-like portions of the basioccipital which, both in my larva and in the adult, support the lateral margins of the parasphenoid, lie dorsal to these processes of the basioccipital and hence in the positions of the bases of the lateral vertebral processes.

Opisthotic. The opisthotic, so named by Traquair, was considered by him to represent both the opisthotic and epiotic of the Teleostei. It has both primary and membrane components and is a much more important bone than in any of the Holostei and Teleostei. It is of irregular shape, forms the dorso-postero-lateral corner of the chondrocranium, and has both external and internal surfaces, the latter forming a posterior portion of the labyrinth recess of the cranial cavity. Its dorsal surface is in articular contact with the ventral surface of the postero-lateral portion of the parieto-dermopterotic, the mesial portion of its posterior surface in contact with the internal surface of the ventro-posterior process of the same bone, and the stout posterior process of the parieto-dermopterotic projects posteriorly between these two articular surfaces. The anterior portion of the dorsal surface of the bone forms the floor of the posterior portion of the temporal groove, and the anterior edge of the bone here shows two directions of growth, one forward along the ridge that forms the lateral wall of the temporal groove and the other antero-mesially across the hind end of that groove and along the outer surface of a slightly raised portion of the chondrocranium which marks the course of the posterior semicircular canal.

Postero-ventrally the opisthotic articulates with the external surface of the basi-exoccipital, a deep and rounded incisure in this edge of the bone forming the anterior boundary of the vagus foramen. The anterior edge of the

bone articulates, in its middle third, with the proötic portion of the ascending process of the parasphenoid, and there forms the posterior boundary of the foramen faciale. The dorsal and ventral thirds of this edge of the bone are both continuous with the cartilage of the chondrocranium, the ventral third being thin and covering the dorso-posterior portion of the small but pronounced swelling of the bulla acustica. This latter part of the bone is perforated, not far from its ventral edge and at the ventro-posterior edge of the bulla, by the foramen glossopharyngeum. A strongly developed opisthotic ridge extends dorso-posteriorly from the anterior edge of the bone to the hind end of its posterior process, and apparently corresponds to the crista facialis and crista parotica, combined, of mammals (Allis, 1920*a*). Dorsal to this ridge there is another, which forms the ventral boundary of the posterior portion of the articular facet for the hyomandibula, this ridge ending posteriorly in a slight process which apparently corresponds to the hind end of the pterotic ridge of the Holostei and Teleostei. Between this ridge and the opisthotic ridge there is a large and slightly concave surface which gives origin to the musculi adductor hyomandibularis, adductor operculi, and levatores arcuum branchialium. The stout posterior process of the bone projects posteriorly in the line prolonged of this concave surface, and gives origin to a stout ligamentous formation which is in part inserted on the distal end of the ventro-anterior process, or so-called pedicel, of the suprascapula, and in part on the dorsal end of the supraclavicula. Ventral to the opisthotic ridge, between it and the bulla acustica, is the large jugular groove. Dorsal to the anterior portion of the opisthotic ridge the lateral surface of the opisthotic forms the ventral portion of the articular facet for the hyomandibula.

On the internal, or cerebral, surface of the opisthotic there are two recesses, a small ventro-posterior one which lodges the hind end of the sinus utriculi posterior, and a large dorso-anterior one which lies in the hollow of the curve of the hind end of the lateral semicircular canal. The lateral and posterior semicircular canals both traverse the bone, the bony canals being in communication with each other at the point where the lateral membranous canal passes internal to the posterior canal. The bone is also traversed by the dorsal, or supratemporal branch of the nervus glossopharyngeus, this nerve entering the bone immediately ventral to the opisthotic ridge and leaving it on its dorsal surface.

In my 75 mm. specimen the opisthotic is but slightly developed. The primary portion of the bone is represented by a thin layer of perichondrial bone which covers that projecting hind end of the otic capsule that lodges the vertically descending portion of the posterior semicircular canal. A few short laminae of bone, of membrane origin, project outward from this perichondrial bone into the surrounding tissues, and on its hind end there is a short posterior process, of membrane origin, which is imbedded in fibrous tissues which extend from there to the overlying dermal bones.

The opisthotic of Polypterus thus has the topographical position of the

opisthotic of other fishes, but it has a much greater extent than that bone has in any other recent fish I know of, having invaded the regions occupied, in those fishes, by the autopterotic, proötic, and epiotic. Pollard (1891) says of this bone that: "In brief the bone is not an opisthotic or intercalare of fish but corresponds to the 'Petrosum' of Urodeles." In a later work, he (1892) still calls this bone the Petrosum in his text, but refers to it in a figure given as the opisthotic. In *Wimania sinuosa*, one of the Coelacanthidae, it is an even larger and more important bone than in Polypterus, and it has been fully described and discussed by Stensiö (1921) both in that fish and in *Bergeria mougeoti*, one of the Palaeoniscidae, Stensiö considering it to be there formed by the fusion of the opisthotic and proötic of the Teleostei and calling it the proötico-opisthotic. Stensiö also discusses (1921, p. 156) the bone in Polypterus, but does not consider that it there contains the proötic.

There is no epiotic in this fish.

What I consider to represent the proötic will be discussed when describing the parasphenoid.

Postfronto-sphenotic. This bone was called by Traquair the postfrontal, and by Bridge and Pollard the sphenotic. It is said by Traquair to consist of two portions, "a posterior, yellowish and spongy-looking, placed like a little vertical plate projecting down from the posterior external angle of the frontal bone; and an anterior part, white and compact, flattened horizontally, and closely applied to the lower part of the frontal, along its external margin behind the orbit." All three of these authors show the bone in figures said to give dorsal views of the cranium with the dermal (investing) bones removed, the bone thus being considered, by all of them, to be a primary ossification.

In my adult specimens the bone is as shown by Traquair, but there is a distinctly evident line along its lateral surface, between the two components noted by Traquair, this line vanishing near the anterior edge of the bone beneath a projecting corner of its superficial component. That part of the bone that lies ventral to this line is of primary origin and represents the sphenotic bone of the Holostei and Teleostei, the part that lies dorsal to the line being of dermal origin and representing the postfrontal of those fishes. Anterior to the anterior end of the line separating these two components, the long anterior process of the bone is also partly of primary and partly of dermal origin, but there is no line of demarcation between the two components.

In my 75 mm. larva the supraorbital band of cartilage forms, as in Budgett's and Lehn's larvae, the entire lateral boundary of the large supraorbital fontanelle. In its posterior portion it is V-shaped in transverse section, as shown in Budgett's figure, the hollow of the V directed dorsally and lodging the anterior end of the otic portion of the main infraorbital latero-sensory canal, which here lies beneath the overhanging lateral edge of the frontal. Posterior to the base of the supraorbital band, the latero-sensory canal is roofed by the anterior end of the parieto-dermopterotic, short laminae of bone being sent down on either side of the canal, thus partly enclosing it. The

parieto-dermopterotic is here completely covered, externally, by the hind end of the lateral edge of the frontal. Immediately anterior to the parieto-dermopterotic, at the base of the supraorbital band, a layer of perichondrial bone has formed on the dorsal edge of the lateral arm of the V-shaped band. From this perichondrial layer, bony laminae, of membrane origin, are sent upward and give insertion, on their lateral surface, to the anterior edge of the musculus levator arcus palatini. These laminae belong to the dermal, or postfrontal component of the bone, and bound laterally the main infraorbital canal, that canal here lying on the dorsal surface of the supraorbital band and being roofed by the lateral edge of the frontal. Continuing forward, in the sections, the main infraorbital canal is soon joined by the hind end of the supraorbital canal (Allis, 1900*a*), and at this point a nerve perforates the supraorbital band and sends a branch to a sense organ that lies in the main infraorbital canal anterior to the point where it is joined by the supraorbital canal, the infraorbital canal here still lying on the dorsal surface of the supraorbital band and not yet being wholly enclosed in the postfrontal component of the postfronto-sphenotic. Continuing forward, the infraorbital canal leaves the dorsal surface of the supraorbital band and acquires a position along its ventro-lateral edge, and it is now wholly enclosed in dermal bone which is continuous with the perichondrial layer developed in relation to the supraorbital band. The supraorbital canal here lies in the frontal, directly above the supraorbital fontanelle. From here forward the infraorbital canal always lies ventro-lateral to the supraorbital band, enclosed in dermal bone that is continuous with the perichondrial layer enclosing that band, and the lateral edge of the frontal overlaps the band externally. The infraorbital canal then leaves the postfronto-sphenotic, to run downward posterior to the orbit, but the supra-orbital band continues onward, lying beneath the frontal and without either dermal or perichondrial bone related to it. The two components of the postfronto-sphenotic are thus apparently completely fused with each other from their very inception, and not simply anchylosed in later stages of development.

In the adult Polypterus the sphenotic component of the postfronto-sphenotic has roughly the shape of a tetrahedron, the base of the tetrahedron directed dorsally and its posterior surface directed postero-mesially and everywhere in primary relation to the cartilage of the chondrocranium. The latter surface nowhere comes into direct relation to the labyrinth recess, but it lies dorso-anterior to the dorso-anterior portion of the anterior semicircular canal. The other two surfaces of the bone are directed the one antero-ventro-mesially and the other laterally, the angle that separates them being presented antero-ventrally and forming the dorso-posterior boundary of the orbital fossa. This edge of the bone is continued forward, as a slight rounded ridge, along the ventral surface of the anteriorly projecting portion of the bone, the latter portion of the bone lying along the lateral edge of the roof of that posterior part of the orbital fossa that is filled by the musculus adductor mandibulae, its anterior end reaching almost to the hind edge of the external opening of the

fossa. The dorsal surface of the bone is large, and has a slightly raised portion along its lateral edge, the deeper-lying portion of the surface lodging and giving support to both the frontal and the parieto-dermopterotic, the former bone occupying approximately the anterior three-quarters of the surface and the latter bone its posterior quarter. The raised and thickened lateral edge of the bone projects laterally slightly beyond the edges of the frontal and parieto-dermopterotic and forms part of the dorsal surface of the skull. Anterior to this raised edge, the bone is entirely covered by the frontal, the lateral edges of the two bones coinciding. The main infraorbital canal, coming up from its course beneath the orbit, enters the bone on its lateral edge at about the anterior quarter of its entire length, and issues from it on its dorsal surface slightly posterior to the middle of the length of that surface. At this point the compound tube 10 infraorbital–7 supraorbital is given off, this tube running antero-laterally, in a curved line, in a groove on the dorsal surface of the bone and issuing through a notch in the lateral edge of the frontal. From the point where this tube is given off, nearly to the hind edge of the bone, the infraorbital canal lies in a deep groove on its dorsal surface, roofed dorsally, in its anterior portion, by the frontal, and posteriorly by the antero-lateral corner of the parieto-dermopterotic, both of these bones resting on the dorsal surface of the postfronto-sphenotic on either side of the canal. In a specimen used in relation to my earlier work on this fish, I found the infraorbital canal enclosed in the postfronto-sphenotic for a short distance posterior to the infraorbital tube 10, a point of bone projecting mesially from the lateral edge of the groove that lodges the canal and fusing with the mesial edge of the groove, thus forming a narrow bridge across it.

Parasphenoid. The parasphenoid is a large and complex bone, and Traquair says that it has been considered to contain, in its anterior portion, the vomer, and in its ascending processes both the proötics and the alisphenoids. He himself concludes that it does not contain either of these three bones, and that it is strictly comparable to the parasphenoid of other fishes. The proötic is said by him to be wholly wanting.

The parasphenoid consists, as in the Holostei and Teleostei, of what may be called a body, and an ascending process on either side, but each ascending process encloses a large canal which, as stated in an earlier work (Allis, 1919*b*, p. 313), corresponds to the canalis parabasalis of the Teleostei. The mesial wall of this canal corresponds to the ascending process of the parasphenoid of Amiurus, and the ventral and lateral walls to the ascending process of Amia and Scomber, and as the process is triangular in transverse section, these three walls may be called the mesial, ventral and lateral plates of the process.

The body of the parasphenoid is a large flat horizontal plate which covers the larger part of the ventral surface of the chondrocranium, the ventral plate of each ascending process projecting laterally and slightly ventrally from it at about the posterior third of its length. Anterior to these processes the lateral edges of the bone converge slightly throughout the full length of

the orbital region, the lateral portions of the bone here forming the floor of the deeper portions of the orbits. Anterior to the orbits the bone widens slightly, and, lying upon the ventral surface of the ethmoidal cartilage, articulates with the hind ends of the palatal plates of the premaxillaries. The extreme anterior end of the bone varies in width in different specimens, and there may here be, on either side, bits of bone that have not yet fused with it. Posterior to the ascending processes, the body of the bone widens slightly to its hind end, and in that end there is a large V-shaped incisure which extends about half the length of this part of the bone. The posterior portion of the basi-exoccipital projects ventrally between the two arms of this incisure, the arms lying along the rounded lateral edges of the basi-exoccipital and extending posteriorly slightly beyond them, there appearing as short processes which project posteriorly along the lateral edges of the first vertebra.

Extending from close to the anterior end of the bone to the level of its ascending processes, there is a well-defined pad of minute thickly-set teeth. This pad has a large anterior end, with an evenly rounded anterior edge, and there occupies the full width of the parasphenoid, but it tapers rapidly and evenly from there to its hind end, where it forms a narrow median band which separates into two curved bands, one on either side, each band running latero-posteriorly along the ventral surface of the curved anterior edge of the ventral plate of the ascending process of its side, and extending nearly to the outer end of that plate. This pad has evidently been developed in relation to the teeth it bears, and the dermal bone so formed has apparently fused with an underlying bone of distinctly different, membrane origin. Between the lateral edges of these two parts of the bone there is a large and rounded groove which receives and gives movable articulation to the dorso-mesial edge of the entopterygoid.

On the dorsal surface of the body of the parasphenoid there is a large median groove, which extends its full length but is somewhat constricted in the pituitary region. At the middle of the length of the pituitary fossa there is a slight median pit, and in a specimen that had been long macerated the bone was here perforated, this thus probably indicating where the epidermal stalk of the hypophysis formerly passed. In the region of the aortic groove the bone is thin in the median line, and in the macerated specimen above referred to this part of it had disintegrated, leaving two long diverging hind ends to the bone. The anterior end of the space between these two ends lies beneath the point where the aortic canal separates into its diverging anterior ends, and hence represents the point where the subaortic process is found in the 75 mm. specimen. For a short distance anterior to this point the parasphenoid is considerably thickened on either side, and this thickened portion is traversed by a deep groove which lodges the basal portion of the related lateral dorsal aorta, the anterior edge of the groove arching posteriorly and forming a partial roof to the groove. This groove runs antero-laterally and opens into the posterior portion of the large canal through the ascending process of the bone.

From near the postero-mesial end of the groove, a small groove leads postero-laterally and opens on the lateral edge of the bone. Anterior to the ascending processes of the bone, each lateral edge of the median groove on its dorsal surface forms a thin ridge which articulates, in its anterior portion with the ectethmoid, and posteriorly with the ventral edge of the sphenoid. At its hind end this ridge curves postero-laterally and is continuous with the anterior edge of the mesial plate of the ascending process of the bone, a large and rounded notch in the latter edge forming the ventral boundary of the anterior opening of a canal in the chondrocranium which I have called, in earlier works, the facialis portion of a trigemino-facialis chamber, but which is more properly called the jugular canal.

The ventral plate of the ascending process of the parasphenoid is triangular in shape, with a convex anterior edge and a concave posterior one. The anterior portion of the anterior edge of the plate is attached by tough connective tissues to the dorsal surface of the dorso-mesial border of the entopterygoid, and it and the lateral edge of the body of the bone anterior to it form the mesial wall and roof of a groove in the dorsal surface of the buccal cavity which leads posteriorly into the oral opening of the spiracular canal, the posterior portion of the edge of the process forming the mesial boundary of the latter opening. The lateral plate of the ascending process rises from the dorsal surface of the anterior edge of the ventral plate, and, projecting dorso-mesially, abuts against and fuses with the external surface of the mesial plate of the process. The mesial plate lies directly upon the cartilage of the chondrocranium, and, in the 75 mm. specimen, is much wider at its base than at its dorsal end, the latter end extending upward along the external surface of the outer wall of the jugular canal and being but slightly wider than it, its hind edge projecting posteriorly slightly beyond the opening of the canal. In the adult this plate still lies along the outer surface of the cartilage that encloses the jugular canal, and, after its fusion with the lateral plate, extends upward until it nearly reaches the ventral edge of the sphenotic portion of the postfronto-sphenotic, the two bones there being separated by a narrow band of cartilage with which they both, apparently, have similar primary relations. In the ventral portion of the hind edge of the plate there is a large incisure, which embraces the anterior edge of the bulla acustica, and anterior to this incisure, or confluent with it, the plate is perforated by a foramen which bounds the anterior opening of the lateral aortic canal of its side. On the mesial surface of the posterior half or two-thirds of the plate, along the line where it fuses with the lateral plate, two flanges of bone have developed, one projecting dorso-mesially along the ventro-mesial surface of the posterior half of the jugular canal and the other dorso-mesially along its lateral and dorsal surfaces, the two flanges arching toward each other and nearly enclosing this portion of the canal (fig. 15). The hind end of each of these flanges projects posteriorly and overlaps externally, and articulates with, the anterior edge of the opisthotic, thus forming the lateral boundary of the foramen faciale. The mesial surface of the

ventro-mesial flange, and the dorsal and lateral surfaces of the dorso-mesial flange, are both in direct contact with the cartilage of the cranial wall, and between the dorso-mesial flange and the dorsal portion of the entire ascending process there is a thick mass of cartilage, that portion of this cartilage that lies anterior to the two flanges being traversed by the anterior portion of the jugular canal. No layer of connective tissue could anywhere be distinguished between these several parts of the bone and the cartilage upon which they lie.

The ascending process of the parasphenoid of the adult Polypterus thus differs greatly from that of the 75 mm. specimen. In the latter specimen all parts of the process are definitely of either membrane or dermal origin, whichever it may be, for the mesial plate of the process is everywhere separated from the cartilage of the chondrocranium by connective tissue, and the ventral and lateral plates have no relations to the cartilage, lying, respectively, internal to the lining membrane of the buccal cavity and to that of the spiracular canal. In the adult, the mesial plate has apparently, in places, acquired primary relations to the cartilage, and the flanges that partly enclose the jugular canal replace, if they do not actually represent the proötic of other fishes, and they probably represent the small and independent bone which both van Wijhe (1882, p. 257) and Stensiö (1921, p. 157) find in this region and which they consider to be a proötic. No part of the bone would seem to contain any part of the alisphenoid.

The canal through the ascending process of the parasphenoid transmits the common carotid artery, a lymph vessel, pharyngeal branches of the nervi glossopharyngeus and vagus and a sympathetic nerve, and the ramus palatinus facialis, after issuing from the jugular canal, runs antero-ventrally across its anterior opening. The canal is thus not the strict homologue of the canalis parabasalis of Amia and the Teleostei, but it certainly represents a part of that canal. The dorsal ends of the efferent arteries of the external hyal gill and the first branchial arch enter the posterior portion of the canal and there fall into the lateral dorsal aorta. The dorsal end of the pharyngo-branchial of the first branchial arch enters the hind end of the angle between the lateral and ventral plates of the process, and is there strongly attached by fibrous tissues; and the pointed posterior corner of this angle gives attachment to a stout ligament which runs posteriorly and is inserted on the dorsal end of the first ceratobranchial. The bulla acustica projects laterally beyond the level of the external opening of the aortic canal, and there closely approaches, and in certain cases touches, the dorsal surface of the parasphenoid, enclosing, in the latter case, a canal between the otic capsule and the parasphenoid. No vessel or nerve was found traversing this canal in the adult, but it is possible that it may be traversed by small arteries related to the thymus. What I consider to be the suprapharyngeal process of the epibranchial of the first branchial arch articulates with the dorsal surface of the bulla, this branchial cartilage being called by Lehn (1918, p. 365) the "Pharyngobranchiale inferius."

The jugular canal is a canal through the cartilaginous postorbital process

which transmits the jugular vein and also a general sensory branch of the nervus trigeminus which joins the truncus hyomandibularis facialis. The primary foramen of the nervus facialis opens into this canal near its hind end, and there may be, anterior to this foramen, an independent foramen for the ramus palatinus facialis. The ramus hyomandibularis issues from the canal through its hind end, the ramus palatinus through its anterior end. The canal thus lies approximately between the primary foramina of the trigeminus and facialis nerves, and hence corresponds to the posttrigeminus portion of some part of the trigemino-facialis chamber of other fishes, and probably to some part of the pars jugularis only of that chamber. The trigeminus part of the chamber lies immediately anterior to this canal, in a recess in the cranial wall that lies beneath the anterior end of the anterior semicircular canal and opens directly into the hind end of the orbital fossa, the posterior portion of the recess being closed externally by the anterior edge of the ascending process of the parasphenoid. The conditions here thus closely agree with those described by Stensiö (1921, p. 177) in *Bergeria mougeoti*—but somewhat differently interpreted by him (see Allis, 1922)—excepting in that the ascending process of the parasphenoid of Bergeria consists of but a single plate of bone, and hence corresponds either to the mesial plate alone of the process of Polypterus, or to the three plates fused so as to appear as a single one. The trigeminus chamber and the jugular canal are both described by Lehn in her 76 mm. specimen, and I, still earlier, described them in a work relating to the arteries of this fish (Allis, 1908*b*).

Sphenoid. The sphenoid bone of Polypterus was so named by Traquair, and was considered by him to be a median bone which occupied the space filled, in the teleostean skull, by the bones called by Huxley the orbitosphenoids, the postsphenoids, and the wings of the latter bones. The bone was said to consist of two vertical laminae connected with each other, posteriorly, by a narrow horizontal plate which formed part of the floor of the cranial cavity. Bridge accepted for this bone the name given to it by Traquair, but Pollard called it the orbitosphenoid. As it certainly contains more than the latter bone, I retain the name given by Traquair.

The internal surface of each vertical lamina of the bone is slightly concave, its outer surface slightly convex. The dorsal edge of the lamina flares slightly (fig. 10), and articulates by dentated suture with the ventral edge of a longitudinal ridge on the ventral surface of the frontal, this latter ridge beginning at the posterior end of the frontal and extending forward, along its mesial third or quarter, nearly its full length. At about the middle of its length this ridge gives off a mesial branch which extends forward a short distance and then curves abruptly to the mesial edge of the bone. When the dorsal edge of the sphenoid reaches the point where this ridge is given off, it expands both laterally and mesially, the lateral portion extending forward but a short distance and there ending abruptly with a straight transverse edge, while the mesial portion curves mesially, widens antero-posteriorly, and, after completely

encircling the nervus olfactorius, meets in the median line its fellow of the opposite side, the two laminae, one on either side of the head, here suturating with each other their full heights. The anterior end of the dorsal edge of each lamina, as seen in the prepared skull, lies on a level with, and is continuous with, the cartilage of the chondrocranium, but ventral to this visible edge the bone continues onward, beneath the cartilage, in an antero-lateral direction, and articulates by suture, at its anterior end and lateral to the canalis olfactorius, with the hind end of the ectethmoid (prefrontal, Traquair). The anterior surface of the bone is everywhere bounded by cartilage, excepting only where it articulates with the ectethmoid.

The surface by which each vertical lamina of the bone articulates, anteriorly, with its fellow of the opposite side is somewhat V-shaped, the V placed horizontally, with its point directed forward (fig. 11). The ventral arm of this V is longer than the dorsal one, and extends to the transverse plane of the foramen opticum, where it curves ventrally and ends in a straight horizontal edge which rests upon the dorsal surface of the parasphenoid. The articulation of the two laminae with each other forms a narrow median wall which lies between the nervi olfactorii and forms the anterior boundary of the median portion of the cranial cavity. Immediately lateral to both the dorsal and ventral arms of this V-shaped median wall, the cerebral surface of each lamina of the bone is slightly hollowed out, this hollow lodging the lobus olfactorius and leading forward to the canalis olfactorius. The floor of this hollow lies above the level of the floor of the pituitary fossa, in the level of the floor of the postpituitary portion of the cranial cavity, and the hind edge of the floor forms, with its fellow of the opposite side, the anterior wall of the pituitary fossa, this raised portion of the cranial floor thus being the homologue of the presphenoid bolster of Gegenbaur's (1872) descriptions of the Selachii.

The ventral edge of each vertical lamina flares somewhat, as its dorsal edge does, but this edge is grooved to form an inverted V, the mesial arm of which is considerably longer than the lateral arm. The hollow of this V rests upon the longitudinal ridge that forms the lateral boundary of the median groove on the dorsal surface of the parasphenoid, the long mesial arm of the V everywhere reaching and resting upon the dorsal surface of that bone, but its external arm not everywhere reaching that surface, the lateral surface of the ridge on the parasphenoid forming, in places, a ventral portion of the mesial wall of the orbital fossa. The lateral arm of the V extends forward to the anterior end of the bone. The mesial arm is abruptly tenoned in the transverse plane of the external opening of the foramen opticum, the V in the ventral edge of the bone anterior to this point being much larger and deeper than it is posterior to it.

The hind edge of each vertical lamina is nearly vertical, inclining slightly anteriorly, and it is everywhere continuous with the cartilage of the chondrocranium excepting at its ventro-posterior corner, where it articulates with the

anterior edge of the mesial plate of the ascending process of the parasphenoid. In this hind edge of the lamina there are two rounded incisures, the dorsal one of which may become entirely enclosed in the bone. The dorsal incisure forms the anterior margin of a foramen which transmits a meningeal vein coming from the dorsal surface of the brain. The ventral incisure forms the anterior margin of the foramen trigeminum, this foramen opening in the cranial cavity dorsal to the proötic bridge (postclinoid wall), slightly anterior to the middle of its width, and being frequently almost entirely, but never entirely, enclosed in the bone. This foramen lies immediately anterior to the anterior wall of the labyrinth recess, and there is here a slight recess on the cerebral surface of the sphenoid. Dorso-posterior to this foramen, the foramen ophthalmicum perforates the cartilage that lies between the sphenoid and the postfronto-sphenotic, and enters the anterior end of the labyrinth recess. From the latter foramen a groove runs dorso-anteriorly along the external surface of the orbital wall, between the sphenoid anteriorly and the postfronto-sphenotic posteriorly, and lodges the ramus ophthalmicus superficialis trigemini, that nerve giving off, while in the groove, the ramus oticus, which pierces the overhanging end of the otic capsule, traverses the canal for the anterior semicircular canal of the ear, and then again perforates the cartilage to issue on the roof of the chondrocranium. Immediately ventral to the ventral edge of the foramen trigeminum, there is a more or less pronounced and rounded notch on the outer surface of the hind edge of the sphenoid, and the nervus abducens, coming from the orbit, traverses this notch and enters a relatively long canal in the cartilage, this canal opening on the floor of the cranial cavity immediately posterior to the base of the postclinoid wall. Anterior to the foramen trigeminum, and in line with it, the sphenoid is perforated by a foramen which transmits the nervi oculomotorius and ophthalmicus profundus, and in a line running dorso-anteriorly from this foramen there are two foramina, the ventral one transmitting the nervus trochlearis and the dorsal one a second meningeal vein from the dorsal surface of the brain. Postero-ventral to the foramen profundo-oculomotorium is the foramen for the pituitary vein, this foramen lying near the ventral edge of the sphenoid and entering the cranial cavity slightly anterior to the anterior edge of the postclinoid wall. In the specimen that was macerated this foramen could not be found on either side of the head. These several foramina were all described in an earlier work (Allis, 1908*b*), and Lehn (1918) describes them in her 76 mm. specimen.

Slightly anterior to the middle of the orbital fossa, at the hind edge of that part of the fossa that is occupied by the eyeball, there is a large notch in the ventral edge of each vertical lamina of the sphenoid. This notch is imperfectly divided into anterior and posterior portions, and it lies beneath a slight swelling on the external surface of the sphenoid. From this notch a canal leads inward in the bone and opens on its cerebral surface dorsal to the hind edge of the presphenoid bolster. This canal transmits the nervus opticus

and the internal carotid artery, and a groove on the internal surface of the sphenoid leads posteriorly from it and marks the further course of the nervus opticus. On both sides of the head of the macerated specimen, a small canal perforated the mesial wall of this canal for the nervus opticus and opened on the internal surface of the sphenoid immediately anterior to the opening of the main canal, this small canal doubtless being traversed by one of the two divisions of the internal carotid. This little canal did not exist in the specimen used for the figures.

Anterior to the anterior end of that portion of each vertical lamina of the sphenoid that lies lateral to the canalis olfactorius, there are, on each side of the head of the specimen used for illustration, two little plates of bone which lie between the sphenoid and the ectethmoid, and there is nothing to definitely show to which one of these two bones they belong. Traquair shows them forming part of the ectethmoid (prefrontal, Traquair), and, following him, I have already referred to the dorsal one of the two as forming part of the ectethmoid. Both plates will accordingly be considered when describing the latter bone.

The hind ends of the two vertical laminae of the sphenoid are connected by the horizontal plate described by both Traquair and Bridge, this plate forming the postclinoid wall and corresponding to the proötic bridge of the Holostei and Teleostei. The dorsal surface of this bridge inclines slightly postero-ventrally, and its ventral surface still more so, the bridge being thicker at its posterior than at its anterior end. Its anterior edge is concave and its posterior edge convex, as Bridge has stated, the hind edge of the bridge projecting posteriorly beyond the hind edges of the vertical laminae of the bone and there being everywhere bounded by cartilage. The hind ends of the vertical laminae are not in contact with each other beneath this bridge, being there separated from each other by cartilage that forms the posterior boundary of the basicranial fontanelle. This fontanelle is large, extends the full length of the pituitary fossa, and corresponds to the fenestra ventralis myodomus of Amia.

In my 75 mm. larva the non-cartilaginous portion of the orbital wall has practically the extent that is shown in Budgett's figure of his 30 mm. larva, extending from near the hind edge of the nasal capsule to a certain distance posterior to the foramen opticum. In Budgett's specimen this portion of the wall was wholly membranous. In my specimen, the posterior and larger portion of this membranous wall has already undergone ossification as membrane bone, and where this membrane bone adjoins the surrounding cartilage, the cartilage is breaking down preparatory to being replaced by bone. There is nowhere any indication either of calcification or of direct ossification of the cartilage. The proötic bridge is, in this larva, a narrow transverse bridge of cartilage which extends the full length of the nervous portion of the pituitary body but does not cover its glandular portion, that portion of the organ being separated from the cranial cavity by membrane only. The conditions in this larva are thus here similar to those in embryos of

Amia, Lepidosteus and certain of the Teleostei (Allis, 1919*b*). The glandular portion of the pituitary body extends to the hind end of the basicranial fontanelle, this hind end lying considerably anterior to the tip of the notochord. In Budgett's 30 mm. larva the fontanelle extended to the tip of the notochord, and the proötic bridge was wholly of membrane. In Budgett's 90 mm. specimen this bridge had become entirely chondrified, and he says that in this specimen the tubules of the glandular portion of the hypophysis are still in communication, by a duct, with the cavity of the mouth. No indication of such a duct was found in my 75 mm. larva, but there is, in the adult, as already stated, a median depression on the dorsal surface of the parasphenoid slightly anterior to the anterior edge of the proötic bridge which doubtless represents the place where the duct has disappeared. Lehn describes (1918, p. 364) this duct in her 76 mm. specimen.

The so-called sphenoid of this fish thus occupies approximately the region of the orbitosphenoids, alisphenoids and median basisphenoid of the Ganoidei and Teleostei, and in addition forms the proötic bridge, which in the Ganoidei and Teleostei is usually (always?) formed by processes of the proötics. What seems to be a strictly similar bone is found in *Bergeria mougeoti* (Stensiö, 1921), one of the Palaeoniscidae, but, singularly enough, is not found in the Coelacanthidae, which are supposed to be much more closely allied to Polypterus. In the Coelacanthidae the proötic bridge is formed by what were formerly considered to be the paired proötics but which Stensiö considers to be a median basisphenoid comparable to that bone of higher vertebrates and hence in no way comparable to the similarly named bone of the Teleostei. Polypterus further resembles the Palaeoniscidae, and differs from the Coelacanthidae, in that its parasphenoid has well-developed ascending processes which lie external to a trigeminus chamber and jugular canal.

Ectethmoid. The ectethmoid (prefrontal, Traquair) is, in the specimen used for illustration, formed by a large and irregular bone which forms the anterior wall of the orbital fossa, and two smaller bones which lie posterior to it. In Traquair's specimen these three bones were apparently fused to form a single bone. The larger bone forms part of the lateral wall of the nasal cavity, and its dorsal surface forms part of the dorsal surface of the primordial cranium, but as the dorso-posterior end of the antorbital process of the premaxillary rests upon it and conceals it, it is not seen in the accompanying fig. 10. The dorsal one of the two smaller bones also forms part of the dorsal surface of the primordial cranium, there lying directly posterior to the larger bone and posterior also to the antorbital process of the premaxillary. Between this small bone and the larger one the preorbital canal leads from the dorso-anterior end of the orbital fossa into the hind end of a short groove on the dorsal surface of the nasal capsule along the mesial edge of the antorbital process of the premaxillary, this groove lodging the ramus ophthalmicus superficialis trigemini, the ramus ophthalmicus profundus, and an accompanying vein and artery. Between the ventral one of the two smaller bones and the ventro-

anterior corner of the vertical lamina of the sphenoid dorsally, and the parasphenoid ventrally, there is the external opening of a small canal which leads into the canalis olfactorius as it leaves the sphenoid bone to enter the nasal capsule, this canal transmitting the terminal portion of the orbito-nasal artery. The ventral surfaces of the ectethmoid and the ventral one of the two smaller bones are covered by cartilage, these bones thus not being exposed on the ventral surface of the chondrocranium. Along the orbital edge of this covering cartilage there is a groove which is continuous with the groove along the lateral edge of the parasphenoid and gives articulation to the articular surface on the anterior edge of the autopalatine.

Visceral arches. There are in Polypterus a mandibular, a hyal, and four branchial arches, and they have been figured and described, in all or in part, by Agassiz (1833–43), Müller (1846), Traquair (1871), van Wijhe (1882) and Pollard (1892). Budgett (1902) has described these arches in a 30 mm. embryo, and I have described the maxillary and premaxillary bones and the labial cartilages in the adult (Allis, 1900*b*, 1919*c*).

Basal line. There is but one piece in the basal line of this fish, the basibranchial of van Wijhe's (1882) descriptions. It is relatively large, and has a flat dorsal and a somewhat concave and irregular ventral surface (figs. 16–19). Its posterior quarter, approximately, is of cartilage and gives articulation to the third and fourth branchial arches. The remainder of the element has become entirely ossified excepting at its anterior end, where it gives articulation to the hyal arch, and at two points on each lateral edge, where it gives articulation to the first and second branchial arches.

The articular facets for the hyal arches occupy the entire anterior end of the element, excepting a narrow median line which separates them. They are oval in shape, the long axis of each facet directed dorso-anteriorly, and they give articulation, through the intermediation of a pad of tough connective tissue, to the hypohyals. The basibranchial is considerably thickened, dorso-ventrally, in the planes of the long axes of these facets, and it is similarly, but less pronouncedly thickened in relation to the articular facets for the second and third branchial arches. Ridges on the ventral surface of the bone run from each of these thickened points toward the middle portion of its anterior third, and there vanish, the ventral surface of the bone thus being concave both longitudinally and transversely. Between the ridges of opposite sides there is a longitudinal groove, which is relatively deep both anteriorly and posteriorly but vanishes in the middle of the length of the bone. Lateral to the ridges of either side, the lateral edge of the bone is much thinner than in its middle portion, and the articular cap for the first branchial arch lies on this thin lateral edge, between the caps for the hyal and second branchial arches; the cap having a shallow facet which is presented laterally and slightly antero-ventrally and gives articulation to the postero-mesial corner of the first hypobranchial. In the specimen used for illustration, this cap was connected with the cap for the hypohyal by a narrow line of cartilage along the

lateral edge of the element. The articular cap for the second branchial arch lies at about the middle of the length of the element, extends from the dorsal to the ventral surface of the element, is slightly 8-shaped, and the facet on its outer surface is presented postero-laterally and gives articulation to the distal end of the second hypobranchial. The posterior, cartilaginous portion of the element is twice as broad and thick in its anterior portion as in its posterior, and is concave transversely on its ventral surface. On either side of its hind end it gives articulation to the fourth ceratobranchial, and on either side of its thickened anterior portion there are two articular facets, separated by a slight groove, which gives articulation to the two articular ends at the distal end of the third hypobranchial.

Branchial arches (figs. 16–21). The hypobranchial of the first branchial arch is, roughly speaking, a thick flat semicircular plate with a stout process arising from the straight edge that forms the diameter of the semicircle, and it is shown in dorsal and ventral views in figs. 20–21. The straight edge forms the distal edge of the element, and the postero-mesial half of the curved edge articulates in part with the ceratobranchial of its arch and in part with the related articular facet on the basibranchial. The process of the element arises from the ventral edge of its straight distal edge, and the ossification of the entire element has apparently proceeded from this point as a centre, semicircular plates of perichondrial bone developing on both sides of the element and giving to it its semicircular appearance. The process is capped with cartilage and strongly attached by ligamentous tissues to the edge of the pad of connective tissue that lies between the articulating surfaces of the hypohyal and basibranchial.

The second hypobranchial has enlarged distal and proximal ends, the longer axes of these ends lying at right angles to each other. The anterior end of the element articulates with the 8-shaped articular facet at the middle of the length of the basibranchial, its posterior end articulating with the ceratobranchial of the arch.

The third hypobranchial resembles the second one in general shape, but has two articular heads on its distal end, these two heads corresponding to the two parts of the 8-shaped articular head of the second hypobranchial, and articulating with the two articular facets at the anterior end of the posterior, cartilaginous portion of the basibranchial.

There is no fourth hypobranchial, as van Wijhe has stated, but the distal portion of the ceratobranchial of this arch forms, in general appearance, a serial continuation of the preceding hypobranchials.

The first ceratobranchial is a stout, strongly curved and flattened bone, capped at each end with articular cartilage. Its distal end lies in a nearly horizontal position, and articulates with the hypobranchial of the arch. Its ventro-lateral (external) edge is not grooved in my large specimens, but is grooved in the 30 cm. ones, and on either side of this edge of the bone there is a row of branchial rays which are wholly of cartilage in my 75 mm. speci-

men, but partly calcified in the adult. The bases of these branchial rays tend to fuse with each other, as shown in fig. 22, and the presence of a double row of rays in this fish, and of but a single row in the Selachii, suggests that the extrabranchials of the latter fishes have been derived either from the basal portions of the anterior row of branchial rays, or from those dorsal and ventral rays of the posterior row that were primarily related to the pharyngeal and hyal elements of the arch. This was explained in a recent work (Allis, 1918*c*, p. 264), but by typographical error a part of the sentence was omitted.

The second ceratobranchial is only about two-thirds as long as the first one, and is less strongly curved. The outer surface of the curve is presented ventrally and is deeply grooved throughout the larger part of its length, the groove lying postero-mesial to an angular process on the antero-lateral edge of the bone, near its distal end. This process is capped with cartilage, and is related to the surface of insertion of the musculus interarcualis ventralis of its arch. The groove on the ventral (external) edge of the bone lodges the afferent artery of the arch.

The third ceratobranchial has much the shape of the second one, but is somewhat shorter and more slender, and the ventro-anteriorly directed process near its distal end is less strongly developed.

The fourth ceratobranchial has strikingly the appearance of being formed by a ceratobranchial and hypobranchial which have not been separated from each other by transverse segmentation. There is no process, capped with cartilage, near the distal end of the ceratobranchial part of the bone, but there is, at that point, a rounded angle on the anterior edge of the bone. Both ends of the bone are capped with cartilage, the distal end articulating with the facet on the hind end of the cartilaginous portion of the basibranchial, and the proximal end articulating, by its anterior corner, with the posterior corner of the cartilaginous cap on the proximal end of the third ceratobranchial. The ceratobranchial part of the bone is grooved on its external edge, exactly as the other ceratobranchials are, but in order to reach this groove the afferent artery of the arch runs postero-laterally across the dorsal surface of the bone, in a groove on that surface, and then turns upward across the posterior surface of the bone, passing through a large opening between it and a series of dermal toothed plates which have fused with it, along the posterior edge of its dorsal surface. The probable explanation of this twisting of the artery around the ceratobranchial is given on a later page.

The epibranchial of the first arch is the bone called by both van Wijhe and Pollard (1891) the suprapharyngobranchial of that arch. Both ends of the element are capped with cartilage, the cap on the distal end being large and articulating by one corner with the proximal end of the ceratobranchial of the arch, and by the other with the so-called infrapharyngobranchial of the arch. An independent bit of cartilage interposed between the epibranchial and ceratobranchial, such as is shown by van Wijhe in his figure and called by him the epibranchial of the arch, was found in certain of the adult specimens

but not in others. In the 75 mm. specimen there is here a little process of the epibranchial, and it is probable that the head of this process sometimes becomes detached, and is found as an independent piece.

The large cartilaginous cap on the distal end of the epibranchial quite unquestionably represents the primitive element, the ossified portion being a process on its postero-mesial edge which corresponds to the suprapharyngobranchial process of the epibranchial of the first branchial arch of Amia (Allis, 1897). This process of the epibranchial of Polypterus forms the principal portion of the element, and it articulates, by its proximal end, with the bulla acustica, there lying in normal position ventral to the vena jugularis. The so-called infrapharyngobranchial is quite certainly simply the pharyngeal element of the arch and is, in the adult, a slender rod of bone which is frequently immovably anchylosed with the epibranchial and apparently has primary relations to the proximal corner of the cartilage that caps that bone and which I consider to represent the primary epibranchial. Between it and the epibranchial, on the external surface of the arch, there is a deep groove, which lies wholly on the epibranchial and lodges the efferent artery of the arch. In the 75 mm. larva, the pharyngobranchial is a slender and wholly independent rod of cartilage which articulates movably with the epibranchial. It lies imbedded in the lateral surface of the thymus, its anterior end extending into the hind end of the angle between the lateral and horizontal plates of the ascending process of the parasphenoid, and there being attached by fibrous tissues. A stout ligament has its origin on the point of that angle, and running postero-laterally, parallel to and slightly ventral to the pharyngobranchial, is inserted on the dorsal end of the ceratobranchial of the arch. In the middle of its length this ligament is, for a short distance, wholly muscular, thus apparently corresponding to that interarcualis dorsalis muscle of the Selachii that extends between the first branchial and hyal arches. The levator muscle of the arch is inserted mostly on the pharyngobranchial, but partly also on adjacent portions of the epibranchial. Comparison of these two elements of this arch of Polypterus with the similarly named elements of the arch in Amia (Allis, 1897), would seem to leave no possible doubt as to their being respectively homologous, the posterior corner of the proximal end of the epibranchial of Amia having, in Polypterus, acquired articulation with the cranial wall instead of with the proximal end of the infrapharyngobranchial of the second branchial arch.

In the second and third branchial arches of Polypterus the epibranchial and pharyngobranchial have fused with each other and are usually both wholly of cartilage. The part that corresponds, in position and in its relations to the efferent artery of the arch, to the epibranchial of the first arch is greatly reduced in length, and its dorso-anterior and dorso-posterior edges have arched toward each other dorsal to the efferent artery of the arch and fused, so forming a short canal through which the efferent artery passes. The pharyngobranchials of these two arches are directed antero-mesially, approximately parallel to

the bony process on the epibranchial of the first branchial arch, and not, as van Wijhe says, posteriorly. In the specimen used for illustration the pharyngobranchial of the second arch had undergone partial ossification.

In the fourth arch there is neither epibranchial nor pharyngobranchial, the anterior corner of the cap of cartilage on the proximal end of the ceratobranchial simply forming a slight process which articulates with the proximal end of the third ceratobranchial.

The branchial arches of this fish are thus strictly comparable to those in Amia. In both fishes the so-called infrapharyngobranchials are simply pharyngobranchials, and there are no independent suprapharyngobranchials in either fish.

The cartilaginous branchial rays (fig. 22) have been referred to in an earlier work (Allis, 1918*c*), and the probable significance of the dorsal ends of the rods formed by the fusion of their bases there considered.

Hyal arch. The hyal arch of Polypterus consists, as currently described, of a hypohyal, ceratohyal, interhyal, and hyomandibula. The symplectic is always said to be wanting. The so-called accessory hyomandibula of certain descriptions was considered by van Wijhe, and since him by other authors, to be one of the series of spiracular ossicles that has become secondarily attached to the hyomandibula.

The hypohyal is a disk-shaped piece, the antero-mesial surface of which is slightly convex and the postero-lateral surface slightly concave. It lies in a nearly vertical plane and its distal edge, which is directed postero-mesially, articulates with the facet on its side of the anterior end of the basibranchial. On its ventral edge, and the postero-lateral surface of that edge, the deeper part of the stout tendon of the musculus sternohyoideus has its insertion, and ossification of the element takes place from the point of attachment of this tendon as a centre, perichondrial plates of bone developing on both surfaces of the element and advancing toward its dorsal edge, the latter edge remaining cartilaginous even in my adult specimens. The superficial portion of the tendon of the sternohyoideus runs forward across the ventral edge of the basihyal and becomes a tough ligamentous formation which envelops the distal end of the ceratohyal, and attached to this ligamentous formation there is a little circular pad of tough tissue which lies between the antero-lateral edge of the hypohyal and the mesial corner of the distal end of the ceratohyal and forms an articular pad between the articulating surfaces of the two elements.

The ceratohyal is a stout flat slightly curved bone with a large distal end, triangular in cross section, and a flat and expanded proximal end which has a long and convex edge. The proximal end of the bone lies in a nearly horizontal position, immediately mesial to and in the horizontal plane of the ventral edge of the hind end of the mandible, but not extending quite to the hind end of that bone. The anterior end of the bone curves slightly dorsally, the ventral surface of the bone thus being slightly convex longitudinally.

Both ends of the bone are capped with cartilage in my small specimens, but in the larger ones ossification tends to extend over the middle portion of the long convex proximal edge of the bone, cartilage persisting only at either end of the edge. The mesial portion of the proximal edge of the bone is covered by a tough pad of fibrous tissue which extends laterally and envelops the distal end of the interhyal of current descriptions, a bone which must represent either the epihyal alone, or both that element and the pharyngohyal (Allis, 1918*c*), and which I shall hereafter call the epihyal. This tissue binds these two bones firmly, but flexibly, together, and certain ligaments have their origins or insertions in it. One of these ligaments is a short one which extends to the internal surface of the gular plate. Another is a relatively narrow band which arises from the ventral portion of the hind edge of the dentary and from the dermarticular immediately posterior to it, and from there runs posteriorly across the ventral surface of the pad on the proximal end of the ceratohyal, there being strongly attached to it. It then turns proximally (here laterally) along the dorsal (internal) surface of the epihyal, and running along that bone, strongly attached to it, reaches and is inserted on the internal surface of the hyomandibula. Beneath (internal to) this ligament is a wider and stouter one which arises from the ventral surface of the dermarticular and running postero-mesially separates into two parts, the mesial one of which is inserted in the pad of fibrous tissue on the proximal end of the ceratohyal, while the lateral one turns dorso-mesially over the lateral portion of the proximal end of the ceratohyal, is there strongly attached to it, and then continues onward and is inserted on the internal surface of the metapterygoid. Beneath this ligament, the hind edge of the fold of epithelial tissue that lies between the floor of the buccal cavity and the ventral surface of the tongue of the fish, is attached, by connective tissue, to the proximal end of the ceratohyal. Beneath the deeper one of the two ligaments above described, and as a part of it, a stout ligament arises from the ventral surface of the articular, and, turning dorsally over its hind edge, is in part inserted on the internal surface of the mandible, but in part continues upward as a short stout ligament which has its insertion on an angular ridge on the internal surface of the quadrate. This ligament and the one inserted on the internal surface of the metapterygoid both pass between the external and internal branches of the ramus mandibularis facialis.

The epihyal is, as shown in figs. 50–52, a small and somewhat cylindrical bone, both ends of which are capped with cartilage. It lies, when the mouth is closed, in a nearly horizontal position, directed postero-laterally and slightly dorsally immediately posterior to the hind end of the mandible. The distal end of the element articulates with the lateral portion of the proximal end of the ceratohyal, and slightly proximal to this articular end of the epihyal there is, on its hind edge, a slight process which gives attachment to the ligamentous formation that binds the two elements together. The summit of this process was of cartilage in one specimen, this seeming to indicate that this process and the actual articular end of the bone together form its distal

end, and that this entire end articulated with the ceratohyal before the two elements acquired the inclined relations to each other that they actually have. The proximal end of the element articulates with the ventro-mesial surface of a process of the cartilage that caps the ventral end of the hyomandibula, the two elements there lying nearly at right angles to each other.

The hyomandibula is, as shown in figs. 29 and 30, a stout flat bone, with two portions which lie nearly at right angles to each other, the dorsal portion directed, from above, ventro-posteriorly, and the ventral portion ventrally and slightly anteriorly. Slightly dorsal to the angle between these two portions, the opercular process projects posteriorly and slightly dorsally, is capped with cartilage, and articulates with an articular facet on the internal surface of the operculum, this facet being lined with cartilage, as van Wijhe has stated. A stout ligament arises from the dorsal edge of the process and is inserted on the ventral edge of the large posteriorly projecting portion of the accessory hyomandibula of Traquair's descriptions. A large depressed region on the anterior portion of the lateral surface of the hyomandibula marks the surface of insertion of the musculus adductor mandibulae. Posterior to this depressed region, the preoperculum lies upon the lateral surface of the bone, and is bound to it by connective tissues.

Both ends of the hyomandibula are capped with cartilage. The dorsal cap articulates with the lateral surface of the cranium in the large hyomandibular facet, the dorsal end of the bone there projecting dorsally beyond the level of the dorsal edge of the large cheek-plate and lying directly internal to the dorsal end of the spiracular canal. The ventral cap has two articular surfaces, one on the ventro-mesial surface of a short pointed process on the posterior end of the cap, and the other on the anterior edge of the anterior end of the cap. The former surface gives articulation to the proximal end of the epihyal. The other surface is a facet which gives articulation to a short process, capped with cartilage, which projects posteriorly from the internal surface of the posterior portion of the quadrate. Dorsal to this latter articulation, the ventral portion of the anterior edge of the hyomandibula fits into a slight groove on the hind edge of the metapterygoid and is bound to it by connective tissues.

There is no independent symplectic, but it is possible that that element is represented in that short articular process of the quadrate that articulates with the anterior surface of the cartilaginous cap on the ventral end of the hyomandibula. This will be discussed when describing the quadrate.

The so-called accessory hyomandibula is a small bone which sits saddle-like on the hind edge of the dorsal arm of the hyomandibula, extending downward from the dorsal end of the arm to the base of the opercular process. The two bones are tightly bound together, and cannot be separated in my non-macerated specimens. The posterior portion of the dorsal end of the bone is exposed on the outer surface of the skull, there lying immediately anterior to the anterior postspiracular ossicle. The dorsal edge of the bone articulates

with the skull in the dorso-posterior portion of the large hyomandibular facet, the articulation being wholly with the lateral edge of the parieto-dermopterotic. The articulating edge of the process was not capped with cartilage on one side of the head of the one adult specimen examined, this being as van Wijhe found it in his specimen. On the other side of the head of my specimen the process was capped with cartilage, this being as Traquair shows it in his figure. On both sides of the head of my 75 mm. specimen there was here a little independent piece of cartilage lying along the dorsal edge of the bone.

The accessory hyomandibula bounds part of the hind end of the spiracular opening, as van Wijhe has stated, and it was considered by him to be one of the series of spiracular ossicles, a conclusion that has been accepted by both Bridge and Pollard. The presence of a bit of cartilage in the articular edge of the bone is decidedly against this supposition, and, as fully discussed in an earlier work (Allis, 1918*c*), I consider this bit of cartilage to represent the dorsal end of the bar formed by the fusion of the bases of the posterior row of branchial rays of the hyal arch, here not completely differentiated to form a posterior articular head to the hyomandibula such as is found in the Teleostei. The ligament that connects the bone that encloses this cartilage with the opercular process represents the ventral portion of the posterior articular head of the teleostean hyomandibula, and the shank of the accessory hyomandibula is a secondary formation of membrane origin. The articular head of the hyomandibula is the homologue of the anterior articular head of the teleostean hyomandibula, and it is derived from the dorsal end of the bar formed by the fusion of the bases of the anterior row of branchial rays of the hyal arch. The ramus hyoideus facialis runs outward between these two heads of the hyomandibula, thus having normal relations to them, but the ramus mandibularis facialis runs outward anterior to the anterior head, which is, so far as I know, an exceptional position in fishes.

Opercular and cheek bones. The larger part of the cheek of this fish is covered by a large and irregular dermal plate which was called by both Müller (1846) and Agassiz (1833–43) the preoperculum. Huxley (1861) says that this bone has two parts, one of which he calls the supratemporal and the other the hyomandibula, and he says that he is much inclined to doubt the existence of a true preoperculum in any crossopterygian fish. Traquair (1871) calls the bone the cheek-plate, and says that the presence of anything corresponding to the preoperculum is somewhat doubtful. Collinge (1893) considers it to be the homologue of the infraorbital bones of Lepidosteus grafted upon the preoperculum, and says that in young skulls these two components of the bone are separated dorsally by a distinct groove, and ventrally by a suture. Pollard (1892) adopts the name preoperculum, but says that the bone consists, as Agassiz first showed, of two parts which correspond to the preoperculum and the lower postorbital of Amia.

This bone of my adult specimens has, as Huxley, Pollard and Collinge all say, decidedly the appearance of being formed of two components, a large

plate-like superficial one, and a deeper one which lies along the mesial surface of the hind edge of the superficial component and projects ventrally beyond it as a stout flat process. There is, however, no suture, at any place in any of my several specimens, separating the two components from each other.

The superficial component is less wide anteriorly than it is posteriorly, its dorsal and ventral edges inclining forward toward the dorsal and ventral edges of the hind end of the maxillary. The more or less convex dorsal edge of the bone is overlapped externally by the series of spiracular ossicles. In the anterior edge of the bone there is a V-shaped incisure which varies in depth but occupies the full length of the edge, the anterior end of the bone thus having two pointed processes, the dorsal one of which overlaps externally the hind end of the maxillary, while the ventral one is overlapped externally by the latter bone. Immediately posterior to the point of the angle in this edge of the bone there is, on the external surface of the bone, a short oval groove which lodges the anterior horizontal cheek-line of pit organs, and both dorsal and ventral to this groove there are slight depressions which, in the fresh specimen, are filled with dermal tissues. In the horizontal line of this groove there is, at the hind edge of the bone, another short groove, which lodges the posterior horizontal cheek-line of pit organs, and perpendicular to the ventral edge of this groove there is a short groove for the vertical line of pit organs. The hind edge of the superficial component forms a slight ledge which runs postero-dorsally in a curved line along the external surface of the deeper component, the dorsal end of the ledge running either into the groove that lodges the vertical cheek-line of pit organs, or, posterior to that groove, into the hind end of the groove that lodges the posterior horizontal cheek-line. The conditions here vary greatly, and it is probably these vertical and horizontal grooves that led Collinge to say that the two components of the bone were separated from each other by a groove. The superficial component of the bone is not traversed by the infraorbital latero-sensory canal and is accordingly the homologue of the so-called squamosal of Glyptopomus and Osteolepis, and not of the postorbitals of Amia (Allis, 1919*e*).

The deeper component of the bone corresponds to the preoperculum of Amia and the Teleostei. Its ventral end is formed by the ventral process of the entire bone, and from there it extends upward along the mesial surface of the superficial component to about one third the distance between the posterior horizontal cheek-line of pit organs and the dorsal edge of the entire bone, where it has the appearance of ending abruptly, with a concave dorsal edge which lies approximately in the level of the axis of the opercular process of the hyomandibula. Up to this point the hind edge of this deeper component lies upon, and is bound by dermal tissues to, the hind edge of the lateral surface of the hyomandibula, and its hind edge is grooved to receive the anterior edges of the operculum and subopercular. Dorsal to this point the internal surface of the cheek-plate is hollowed out to receive the articular end of the operculum and to give passage to the musculus dilatator operculi, and dorsal to this

hollow, the dorsal edge of the entire bone is somewhat thickened, and forms an eminence, or short process, which is directed dorso-postero-mesially and gives attachment to tissues of the region.

The preoperculo-mandibular latero-sensory canal enters the ventral end of the process-like ventral end of the cheek-plate, and runs upward in the plate to its dorsal edge, thus passing upward beyond its thickened, preopercular portion. At the dorsal end of the ventral, process-like portion of the bone, tube No. 7 of the line is given off, tube No. 8 being given off directly posterior to the posterior horizontal cheek-line of pit organs. Dorsal to the thickened, preopercular portion of the bone, the canal turns dorso-anteriorly and traverses the superficial, plate-like portion of the bone, approximately along the bottom of the hollow that lodges the articular end of the operculum and the musculus dilatator operculi. This part of the canal contains no sensory organ, the dorsal organ of the line lying in the dorsal end of the deeper, thickened part of the bone. That part of the canal that lies dorsal to this thickened portion has thus apparently been secondarily enclosed in a part of the entire bone that does not belong to the preoperculum.

The bone *Y'* of Traquair's descriptions I do not find in any of my specimens, unless it be that it is represented in the anterior prespiracular ossicle.

The bone *Y''* is always present, and in all my large specimens there is a second and similar bone posterior to it, as shown in Müller's (1846) figure of this fish, the external surfaces of both bones being tuberculated. In the small specimens of *Polypterus Lapradei* the anterior bone, only, was found, this being as shown in Traquair's figure of his specimen of *Polypterus senegalus*. The two bones usually lie ventral to the ventral edge of the cheek-plate, but may somewhat overlap that edge.

The operculum (fig. 33) is a large bone with a rounded hind edge marked with concentric lines. The ventral portion of the anterior end of the bone fits into the groove on the hind edge of the deeper component of the cheek-plate, and immediately dorsal to this part of the bone is the facet for the opercular process of the hyomandibula. This facet is lined with cartilage and is presented antero-mesially, this being the only bony fish I know of in which this facet is said to be lined with cartilage, excepting only Alepocephalus (Gegenbaur, 1878). The operculum projects anteriorly somewhat beyond this facet, and is there hollowed out on its internal surface. On the internal surface of the anterior edge of this part of the bone the tendon of the musculus dilatator operculi has its insertion. The dorsal edge of the operculum is overlapped externally by the ventral edges of the postspiracular ossicles, the dorsal edge of the operculum being slightly grooved, on its external surface, to receive them.

The suboperculum articulates, along its anterior edge, with the hind edge of the cheek-plate, its dorso-posterior edge being overlapped externally by the antero-ventral edge of the operculum.

Palatoquadrate. The palatoquadrate (figs. 29 and 30) is an elongated struc-

ture, traversed its full length by a band of cartilage which is bounded dorsally, ventrally and internally by bone, its external surface alone being exposed. The dorsal edge of the apparatus is strongly convex and lies in a nearly horizontal position, its anterior two-thirds fitting into the groove on the lateral edge of the orbital portion of the parasphenoid, between its membrane and tooth-bearing components, and being bound to it by connective tissues, and its posterior third turning outward and lying along the lateral surface of the ventral end of the spiracular canal. The hind end of the apparatus is double, the two ends being parallel and separated by a slight groove, but their hind edges lying at a considerable angle to each other. The internal one of these two edges extends downward from the dorsal edge of the apparatus to about the middle of its width, and abuts against and is firmly bound to the anterior edge of the ventral portion of the hyomandibula. The external one of the two edges extends the full width of the apparatus, inclining antero-ventrally and overlapping externally, at its dorsal end, the anterior edge of the hyomandibula. The posterior portion of the ventral edge of the apparatus is bent outward at approximately a right angle to the anterior portion, lies in a transverse position, and forms the articular surface for the mandible. Starting from the outer end of this bent-out edge, a ridge runs upward on the external surface of the apparatus, approximately in the transverse plane of the anterior edge of the postorbital process of the chondrocranium, and marks both the posterior limit of the surface of origin of the deeper portion of the musculus adductor mandibulae, and the anterior limit of the surface of origin of the superficial portion. Immediately anterior to this ridge, and slightly ventral to the middle of its length, there was, in two of the four specimens examined, but not in the other two, the external opening of a canal which ran dorso-posteriorly in the apparatus. It did not issue on the internal surface of the apparatus, and nothing was found entering it. The bending outward of the ventral edge of the apparatus forms a deep depression on its external surface, the anterior edge of the depression being marked by a lateral process on the ectopterygoid. The transverse plane of the angle of the gape lies immediately posterior to this process, between it and the anterior edge of the ascending process of the splenial, and when the mouth opens and shuts, the splenial, with the attached labial cartilage and related tissues, has a sliding dorso-ventral motion on the hind edge of the lateral process of the ectopterygoid. The anterior end of the cartilaginous core of the apparatus has ossified as the autopalatine, and this bone, capped with cartilage, articulates with the cartilage that covers the ventral border of the orbital surface of the ectethmoid.

The quadrate was, in the specimen particularly examined, so firmly bound to the metapterygoid that the two bones could not be separated without breakage. The bone is quadrantal in shape, with one edge lying in a horizontal plane and the other directed dorso-postero-mesially, and its external surface is crossed by the ridge, above described, that forms the boundary between the surfaces of insertion of the deeper and superficial portions of

the adductor mandibulae. The ventral edge of the bone is curved, with its posterior portion transverse in position, and this part of the edge articulates with the autarticular in a transverse groove on the dorsal surface of that bone, neither of the articular surfaces being capped with cartilage so far as could be determined from my specimens.

On the internal surface of the bone there is a pronounced ridge which begins, ventrally, at the mesial end of the articular edge of the bone, and runs dorso-posteriorly nearly to its dorsal edge. There it turns posteriorly, or postero-ventrally, and extends to the hind edge of the bone, there forming the ventral end of the mesial one of the two diverging hind edges of the dorsal portion of the entire apparatus. Between this ridge and the hind edge of the bone there is a deep depression which receives the hind end of the autarticular when the mouth is widely opened. That part of the ridge that forms the ventral end of the mesial one of the diverging hind edges of the apparatus is capped with cartilage that is continuous with the cartilaginous core of the apparatus, and, as already stated, it articulates with the anterior edge of the cartilaginous cap on the ventral end of the hyomandibula. The ramus mandibularis externus facialis passes external to this process-like part of the quadrate, the ramus mandibularis internus passing internal to it, the process thus having to these two nerves and to the hyomandibula and quadrate, the relations that the teleostean symplectic would have if it were to fuse with the quadrate instead of with the hyomandibula; and it is quite probable that it represents some part of that element of the hyal arch.

The convex dorsal edge of the quadrate is everywhere bounded by cartilage. Its internal surface, anterior to the ridge across it, is completely covered by the metapterygoid and ectopterygoid, these two bones resting directly upon it, and the metapterygoid being firmly anchylosed with it in the one specimen examined.

The metapterygoid has, in my adult specimens, decidedly the appearance of being wholly an investing bone, and in the 75 mm. specimen it at no place has primary relations to the cartilage of the apparatus, this thus confirming van Wijhe's and Pollard's conclusions regarding it. It lies mainly upon the internal surface of the apparatus, but its dorsal edge embraces the dorsal edge of the cartilaginous core and projects somewhat above it, there being exposed on the lateral surface of the apparatus. The anterior portion of this dorsal edge is grooved on its dorso-lateral surface, and there receives and articulates with the hind end of the entopterygoid. On the mesial surface of the apparatus the bone articulates anteriorly with both the ectopterygoid and entopterygoid, and ventrally with the quadrate, overlapping the mesial surface of the latter bone to a considerable extent and being itself overlapped mesially by the entopterygoid, the latter bone fitting into a sharply marked depression on the mesial surface of the metapterygoid.

The hind edge of the bone is slightly thickened and grooved, and lodges part of the cartilage, already referred to, that forms the ventral portion of the

mesial one of the two hind edges of the entire apparatus. The dorso-posterior corner of that part of the bone that overlaps externally the dorsal edge of the cartilage of the apparatus is either perforated by a foramen, or deeply notched in its hind edge. This foramen, or notch, is traversed by the ramus mandibularis internus facialis, that nerve then running downward between the cartilage of the apparatus and the internal plate of the metapterygoid and issuing at the ventral edge of the latter bone, between it and that process of the quadrate that apparently corresponds to the symplectic. The dorso-anterior portion of the mesial surface of the bone is roughened with minute tooth-like eminences.

The entopterygoid is a long thin dermal bone which forms the larger part of the dorso-mesial edge of the apparatus, there projecting considerably beyond the cartilage of the apparatus. Ventral to this wide projecting edge, the bone rests upon the mesial surfaces of the metapterygoid and ectopterygoid, lying in a sharply marked depression along the dorsal edges of those bones, and being separated, by them, from all contact with the cartilaginous portion of the palatoquadrate. The anterior half of the dorso-mesial edge of the bone is loosely bound to the lateral edge of the parasphenoid, between its membrane and tooth-bearing components, the posterior half lying against the external surface of the spiracular canal. The anterior end of the bone is thin, and extends forward onto the ventral surface of the posterior portion of the ethmoidal cartilage, there being covered by tough connective tissues. Its hind end is somewhat pointed, curves postero-laterally, and rests upon the dorso-external surface of the dorsal edge of the metapterygoid. Its mesial surface is completely covered with small tooth-like eminences, excepting that part of its anterior end that extends forward beneath the ethmoidal cartilage.

The ectopterygoid is a thin dermal bone which lies directly upon the mesial surface of the cartilage of the palatoquadrate, its dorsal edge coinciding with the dorsal edge of that cartilage, but its ventral edge extending ventrally beyond the cartilage. The mesial surface of the bone is everywhere covered with small tooth-like eminences, these eminences becoming small sharp teeth along the anterior half of its ventral edge and there forming a posterior continuation of the teeth on the oral surface of the mesial dermo-palatine, the so-called vomer of earlier descriptions. The dorsal edge of the bone is overlapped to a considerable extent by the ventral edge of the entopterygoid, as just above explained. Its hind end overlaps slightly the anterior edges of the metapterygoid and quadrate.

The anterior end of the ventro-lateral edge of the ectopterygoid is somewhat thickened, apparently by dermal accretions to its external surface, this giving rise to what appears like a short antero-laterally projecting process, this process and the remainder of the bone being separated by a narrow V-shaped space which receives the hind edge of the palatine process of the maxillary. The anterior end of the body of the ectopterygoid, which forms the ventro-mesial boundary of this V-shaped space, articulates with the hind end

of the mesial dermopalatine, the antero-laterally projecting process giving support, on its dorsal surface, to the autopalatine. This little process may accordingly be called the palatine process of the ectopterygoid, and posterior to it, at the hind end of the row of small sharp teeth on the anterior portion of the ventral edge of the bone, there is a second process, which I have above referred to as the lateral process of the bone. This process is directed laterally and has a flat and somewhat spreading outer end which abuts against, and is firmly bound to, the ventral portion of the internal surface of the maxillary, immediately posterior to the toothed part of that bone (Allis, 1900*b*). The posterior edge of the process is slightly hollowed and gives sliding articulation to tissues attached to the anterior edge of the ascending process of the splenial. Dorso-anterior to the base of this process there is a large semicircular notch in the ventral edge of the cartilage of the palatoquadrate, the lateral surface of the ectopterygoid there being exposed. This notch lies beneath the eyeball, and is apparently caused by the wearing action of that organ. The bone is here traversed by a small canal which begins at the dorsal edge of the palatoquadrate cartilage and issues near the ventral edge of the ectopterygoid, the canal transmitting a branch of the ramus palatinus facialis, which thus has the course of the ramus palatinus posterior facialis of Amia. In Amia that nerve runs antero-ventrally across the external (dorso-lateral) surface of the entopterygoid, passes internal to the cartilage of the palatoquadrate, and then internal to the autopalatine, between it and the dermopalatine, sometimes perforating the autopalatine in part of its course. The conditions in Polypterus would accordingly arise if the autopalatine of Amia were to be pushed forward beyond this nerve, and the nerve were then to become enclosed in the dermopalatine, this suggesting that the dermopalatine of Amia is represented in the anterior portion of the ectopterygoid of Polypterus.

The autopalatine is a small bone of primary origin which develops in the anterior end of the palatoquadrate cartilage, that end of the cartilage here turning slightly antero-laterally. The bone rests upon the dorsal surface of the palatine process of the ectopterygoid, and was not, as van Wijhe found it, fused with that process in any of my specimens. Its slightly concave dorsal surface is capped with cartilage and articulates with the cartilage that covers the ventral surface of the ectethmoid. The ethmopalatine ligament of Pollard's descriptions (1892, p. 413) arises from the cranium posterior to this articular surface and, running postero-laterally and spreading considerably, is inserted along the dorso-mesial edge of the cartilaginous core of the palatoquadrate. Pollard says that this cartilaginous core projects forward beyond the autopalatine, and that this anterior portion is the homologue of the prepalatine cartilage of his descriptions of the Siluridae. No such projecting portion of the cartilage was found in any of my specimens.

Van Wijhe (1882, p. 253) found the autopalatine fused with the anterior end of the ectopterygoid, as above stated, and because of this he concluded that this anterior portion of the latter bone fulfilled the function of a dermo-

palatine, and was hence probably, genetically (in der Entwickelungsgeschichte), an independent bone, the equivalent of the dermopalatine of the Ganoidei, a conclusion which the relation of the ramus palatinus posterior facialis to the bone seems to fully confirm, as just above explained.

The mesial dermopalatine (figs. 23–27), the so-called vomer of earlier authors, forms a direct anterior prolongation of the ventro-lateral portion of the ectopterygoid. It is furnished with small sharp teeth, and its posterior portion lies upon and is firmly bound to the ventral (oral) surface of the palatine process of the maxillary, its anterior end projecting forward beyond that process and lying upon the ventral (oral) surface of the palatine process of the premaxillary, but only loosely bound to it. This end of the bone is somewhat wider than its posterior portion, and curving mesially meets and articulates, in the median line, with its fellow of the opposite side. The curved external edge of the bone is concentric with the line of the premaxillo-maxillary teeth, and separated from them by a groove which I have called the primary alveolo-labial sulcus (Allis, 1919*c*). Along the postero-mesial edge of the bone there is a slight furrow in the lining membrane of the roof of the buccal cavity, and I formerly, but erroneously, considered the anterior edge of this groove to represent the maxillary breathing-valve of the Teleostei. This bone thus being a mesial dermopalatine, the dermopalatine of Amia, which is represented in the anterior portion of the ectopterygoid of Polypterus, must be a lateral dermopalatine.

Mandible. The mandible contains the four bones described by Traquair, and also the mento-Meckelian ossicle described by van Wijhe. No bone corresponding to the angular of van Wijhe's descriptions was found in any of the specimens examined, nor was there any indication of such a bone having fused with the dermarticular.

The dentary is a long and rather slender bone, the anterior end of which curves mesially. It bears on its dorsal edge a single row of sharp stout teeth. Its mesial surface is deeply grooved its entire length, the anterior half of this groove being relatively narrow, with an enlarged anterior end, and lodging the anterior portion of Meckel's cartilage and the mento-Meckelian ossicle. The posterior portion of the groove is deeper than the anterior portion, and widens gradually to the hind end of the bone, there occupying its entire width and lodging the anterior portion of the dermarticular. The mesial surface of the dorsal edge of the groove is flat and articulates with the lateral (aboral) surface of the ventral half of the anterior portion of the splenial, the latter bone projecting dorsally above the articulating surface with the dentary and forming a pronounced ridge which lies parallel to the outer, tooth-bearing edge of the dentary and is separated from it by a deep groove which lodges the ramus mandibularis internus facialis and a branch of the ramus mandibularis trigemini that I consider to represent part of the ramus posttrematicus internus of the nerve. In the hind edge of the dentary there is a large V-shaped incisure, the sharp dorsal and ventral edges of the incisure resting upon the

external (lateral) surface of the dermarticular. The anterior end of the bone is thickened, turns slightly mesially, and has a large flat surface which articulates with its fellow of the opposite side. The ventral edge of this part of the bone is flattened and projects slightly ventrally as a sharp ridge, but there is no indication that this part of the bone was, as van Wijhe suggests, a primarily independent predentary that has fused with the dentary.

The dentary is traversed its full length by the mandibular latero-sensory canal, the canal entering the bone on its external surface, close to the symphysis, and leaving it at the re-entrant point of the large V-shaped incisure in its hind edge. Two tubes leave the canal as it traverses the bone, and the bone lodges three sense organs of the line. The ramus mandibularis externus facialis runs forward ventral to the groove that lodges Meckel's cartilage, and three short canals give passage to the branches sent to the three sense organs lodged in the bone.

The dermarticular is a stout dermal bone, with a long and sharply pointed anterior end which fits into the posterior portion of the groove on the mesial surface of the dentary, the outer surface of the dermarticular being excavated to receive the diverging hind ends of the dentary. Posterior to the dentary the ventral edge of the bone is thin, and on the external surface of this edge, immediately posterior to the hind end of the dentary, there is a small pit-like depression which is presented ventrally and forms part of the surface of origin of the long ligament that has its insertion on the proximal (posterior) end of the ceratohyal. On the mesial surface of the bone there is a groove to receive the posterior portion of Meckel's cartilage, and this groove is crossed by a smaller groove which lodges the ramus mandibularis externus facialis and the ramus mandibularis trigemini as those two nerves run forward onto the mesial surface of the dentary. Dorsal to the posterior portion of this latter groove there is a depression which forms the surface of insertion of a part of the musculus adductor mandibulae. Ventral to the hind end of Meckel's cartilage the ventral edge of the groove that lodges it rises as a ridge-like process, the mesial surface of which is flat and roughened and articulates with the aboral surface of the ventral edge of the splenial. Posterior to this, the mesial surface of the dermarticular articulates with the lateral surface of the autarticular, the dorsal edge of the bone projecting upward beyond this surface of articulation and there articulating with the ventral edge of the lateral plate of the ascending process of the splenial.

The dermarticular is traversed by the posterior portion of the mandibular latero-sensory canal, and lodges two organs of that line. The canal enters the bone on its external surface at the point of the V-shaped incisure in the dentary, and leaves it near its dorsal edge close to its hind end, one tube leaving the canal as it traverses the bone. Slightly dorso-anterior to the opening by which the canal leaves the hind end of the bone, there is a notch in the edge of the bone, this notch leading into a canal which runs forward, at first between the dermarticular and the autarticular and then through a portion of the former

bone to reach and enter the little groove that crosses the groove that lodges Meckel's cartilage, this canal transmitting the ramus mandibularis externus facialis.

The autarticular (figs. 38 and 39) is an irregular bone which lies between the hind ends of the dermarticular and splenial, articulating with the former bone by its entire lateral surface excepting only a narrow dorso-posterior edge, and with the splenial by the anterior third or half of its mesial surface. The hind end of Meckel's cartilage abuts against the anterior end of the bone, and is in primary relations to it. At about the middle of the length of the dorsal surface of the bone there is a transverse hour-glass shaped groove which is lined with connective tissue and not with cartilage and gives articulation to the articular edge of the quadrate. These two articulating surfaces are thus neither of them lined with cartilage. Anterior to this articular groove, the dorsal surface of the autarticular is deeply grooved, this groove occupying the entire dorsal surface of the bone and inclining antero-ventrally into the hollow of the mandible. Posterior to the articular groove the bone narrows abruptly and then tapers to a rounded hind end which is capped with a pad of tough connective tissue which looks somewhat like cartilage and rubs against the anterior edge of the epihyal. On the mesial surface of the bone, immediately ventral to the mesial end of the articular facet for the quadrate, there is the external opening of a short canal which traverses the bone and transmits the ramus mandibularis internus facialis.

The mento-Meckelian ossicle is a small cylindrical, or knob-shaped bone which extends from the anterior end of Meckel's cartilage forward to the symphysis, where it articulates with its fellow of the opposite side. It lies in the enlarged anterior end of the longitudinal groove on the mesial surface of the dentary and is not seen in either lateral or anterior views of the latter bone.

Meckel's cartilage is a rod-shaped piece which extends from the autarticular to the mento-Meckelian ossicle. In its posterior portion it is flat, and there lies against the mesial surface of the dermarticular. Anteriorly it becomes gradually rounded, and there lies in the longitudinal groove on the mesial surface of the dentary.

The splenial (fig. 28) is a long dermal bone which is best described as formed of two thin plates, one lateral and the other mesial, the lateral plate being narrower than the mesial one and not extending as far posteriorly. In the anterior half of the bone the two plates have a common dorsal edge and are completely fused with each other. Posteriorly the ventral portions of the two plates diverge from each other, but their dorsal edges remain fused, and the two plates are produced dorsally to form the tall ascending process of the bone. The lateral surface of the mesial plate here rests upon the flattened mesial surfaces of the autarticular and dermarticular, the ventral edge of the lateral plate resting upon the dorsal edges of the lateral surfaces of those same bones. The ascending process is thus deeply grooved both ventrally and posteriorly, and straddles the posterior opening of the ramus of the mandible,

the floor of that opening being formed by the concave dorsal surface of the prearticular portion of the autarticular. Anterior to the ascending process, the mesial plate of the splenial rests against the mesial surface of the ridge that forms the dorsal edge of the groove in the dentary that lodges Meckel's cartilage, the ventral edge of the lateral plate resting upon the dorsal surface of that ridge. Anterior to the anterior end of the splenial there are the two little dermal and toothed plates described by van Wijhe, and these plates and the dorsal edge of the splenial form the mesial boundary of the deep groove that is bounded laterally by the tooth-bearing edge of the dentary, that groove extending from the anterior edge of the base of the ascending process forward to the symphysis and there being continuous with the groove of the opposite side. The mesial surface of the splenial, and the base of its ascending process are covered with minute tuberosities.

The ascending process of the splenial, together with the labial cartilage and related tissues, has sliding articulation with the posterior edge of the lateral process at the middle of the length of the ectopterygoid. On its dorsal and posterior edges it gives insertion to the masseter division of the musculus adductor mandibulae, and anterior to that muscle to the tough connective tissues that envelop the labial cartilage. There is no cartilage whatever in the process, even in my 75 mm. specimen, and I can see no reason to assume, as van Wijhe has suggested was probable, that any part of it is, or has been derived from, a primary ossification. The process would seem to correspond strictly to the coronoid (operculum) bone of certain reptiles (Baur, 1895, fig. 3), and is certainly in no way related to the cartilaginous coronoid process of Amia.

Maxillary. This bone of the adult Polypterus has been formed by the fusion of two suborbital latero-sensory ossicles with a dental bone that quite certainly corresponds to the maxillary component of the superior maxillary bone of mammals (Allis, 1900*b* and 1919*c*). Projecting mesially from the mesial surface of the anterior portion of the bone there is a long and thin palatine process which rests directly upon the ventral surface of the ethmoidal cartilage, but is only loosely bound to it. The mesial half of the ventral (oral) surface of this process supports, and is immovably attached to, the posterior two-thirds, approximately, of the mesial dermopalatine and to the anterior end of the ectopterygoid. The bone bears a single row of stout sharp teeth, and the hind end of this tooth-bearing part of the bone rests against the antero-ventral edge of the lateral process of the ectopterygoid, the lateral end of the latter process resting against the mesial surface of the maxillary dorso-posterior to this point, and being firmly but not immovably bound to it by a short stout ligament. All movements of the palatoquadrate are thus impressed upon the maxillary, and *vice versa.*

The maxillary articulates anteriorly with the premaxillary and lachrymal, and posterior to those bones forms the larger part of the ventral boundary of the orbit. Its dorso-posterior corner is overlapped externally by, and loosely attached to, the postorbital bone and the anterior spiracular ossicle.

The dorsal portion of the hind end of the bone projects posteriorly as a long and pointed process which fits against the internal surface of the large cheek-plate, the ventral portion of the bone projecting as a shorter process which lies against the external surface of the cheek-plate. These two bones and the palatoquadrate and hyomandibula are thus all firmly but apparently not immovably bound together. The anterior one of the two bones *Y''* lies external to the ventro-posterior corner of the maxillary.

The dorsal portion of the maxillary is traversed by the infraorbital latero-sensory canal, that canal entering the bone close to its dorsal edge, at the hind end of the lachrymal, and issuing from it on its external surface near its dorsal edge and immediately ventral to the postorbital bone. One primary tube is given off as the canal traverses the bone, and issues from it dorsal to the hind end of the line of maxillary teeth. The bone lodges two sensory organs of the line.

Premaxillary. This bone, like the maxillary, is formed by the fusion of latero-sensory and dental components, and also like the maxillary it has a flat palatine process, of membrane origin, which rests upon the ventral surface of the ethmoidal cartilage. This palatine process projects posteriorly and articulates with the anterior edge of the parasphenoid, and between it and its fellow of the opposite side there is a small exposed portion of the ventral surface of the rostral process of the chondrocranium. The internal surface of the premaxillary rests against the anterior edge of the rostral process, the bone projecting dorso-posteriorly above that process, and the internal (here posterior) portion of its dorsal edge there articulating with the anterior edge of the median ethmoid. Lateral to the latter bone the premaxillary sends a small ascending process dorso-postero-mesially, this process lying in the groove along the lateral surface of the head of the ethmoid and giving support, on its dorsal end, to the antero-mesial corner of the nasal, and partly also to the mesial end of the os terminale. Lateral to this process, the dorsal surface of the premaxillary is slightly hollowed out and forms the ventral edge of the fenestra nasalis, this part of the premaxillary lying beneath the antero-lateral portion of that atrial chamber of the nasal sac from which the anterior and posterior nasal tubes have their origins. Lateral and posterior to the fenestra nasalis the premaxillary has a stout antorbital process which projects dorso-posteriorly along the lateral edge of the fenestra nasalis, there lying against the lateral surface of the nasal capsule and giving support, on its dorsal end, to the lateral edge of the nasal and the antero-lateral corner of the frontal. Postero-ventrally the process articulates both with the ectethmoid and the lachrymal, and ventral to the latter bone with the anterior end of the maxillary. The bone has a single row of stout sharp teeth which apparently correspond to the premaxillary teeth of mammals (Allis, 1919*c*).

The premaxillary is traversed by the preorbital portion of the infraorbital latero-sensory canal, that canal entering it on its dorsal surface at the lateral edge of the median ethmoid, and leaving it at the anterior edge of the lachry-

mal. Two primary tubes leave the canal as it traverses the bone, the lateral one lying dorsal to the hind end of the row of premaxillary teeth. The bone lodges three organs of the infraorbital line, which correspond to those in the antorbital and the lateral half of the median ethmoid of Amia.

Latero-Sensory Canals

These canals were fully described in an earlier work (Allis, 1900*a*), and as their relations to the individual cranial bones have already been given in the present work, and the manner of their innervation will be given when describing the nerves, it will suffice to here give simply their general course and disposition.

The accompanying fig. 1 gives a full length view of a 44 cm. specimen of *Polypterus bichir*, and shows the external openings of the primary tubes of the cranial canals, the line of little grooves that mark the positions of the sensory organs of the lateral line of the body, and other similar grooves that mark the positions of other lines of surface organs. Figs. 2, 3 and 4 give enlarged lateral, dorsal and ventral views of the same specimen. Comparing these figures with those of the prepared skull of the 49 cm. specimen (figs. 5 and 6), it is seen that most of the surface pores of the canals lie in a thick dermis which completely covers all those bones the external surfaces of which are without rugous markings, and also the smooth and bevelled edges of certain of the other bones.

The supraorbital canal begins at a pore that lies immediately posterior to the base of the nasal tube, approximately in the line prolonged of the three suborbital pores of the main infraorbital line. From there the canal enters and traverses the os terminale, and at its antero-mesial end anastomoses with the second primary tube of the main infraorbital canal, there forming the double tube and pore 2 inf.–2 sup. Turning posteriorly from there the supraorbital canal enters and traverses, successively, the accessory nasal, nasal and frontal, issuing from the latter bone near the hind end of its lateral edge and there anastomosing with the main infraorbital canal to form the double tube and pore 10 inf.–7 sup. There are six sensory organs in the line, and seven primary tubes and pores.

The main infraorbital canal begins in the median line on the top of the snout, and is there in direct continuation with its fellow of the opposite side of the head. There is no median pore marking the point of fusion of these two canals, this probably being due to the fact that the anterior sensory organ of each line lies so close to the median line, that the two organs were enclosed simultaneously in the process of involution that gave origin to the canal, no primary tube ever forming between them. Starting from this point the canal traverses the ethmoid, and on issuing from that bone anastomoses with the supraorbital canal to form the double tube and pore 2 inf.–2 sup. The canal then enters and traverses, successively, the premaxillary, lachrymal, maxillary, postorbital and postfronto-sphenotic, and on the dorsal surface of the latter bone becomes a groove which is roofed in its anterior portion by the frontal

and in its posterior portion by the parieto-dermopterotic. Slightly anterior to the line between these two latter bones the canal anastomoses with the hind end of the supraorbital canal, a single double tube and pore, 10 inf.–7 sup. marking the point of fusion. Posterior to this point the canal enters the parieto-dermopterotic, traverses that bone and then the second and first supratemporals and the posttemporal, at the hind end of which it comes to the surface and ends. While traversing the second supratemporal, or between that bone and the first supratemporal, it anastomoses with the lateral end of the supratemporal cross-commissure, so forming the double tube and pore 12 inf.–1 supratemporal. There are 13 sense organs in all in the line, and 13 primary tubes and pores, the anterior tube and pore of the line not being present.

The supratemporal commissure traverses the second and third supratemporal bones, and anastomoses in the median line with its fellow of the opposite side, a single median pore marking the point of fusion. There are two sense organs in the line, and three primary tubes and pores, counting the two terminal ones.

The preoperculo-mandibular canal begins at the symphysis of the mandibles, at a median pore common to it and its fellow of the opposite side. From there the canal runs posteriorly through the dentary and dermarticular, traverses the dermis between the latter bone and the ventral end of the preoperculum, and then turns upward in the latter bone, traversing it and ending at a pore that lies on the external surface of the cheek-plate near its dorsal edge. The canal does not reach and anastomose with the main infraorbital canal, this doubtless being related to the presence of the line of spiracular ossicles. There are eight sense organs in the line, five in the mandible and three in the preoperculum, and there are nine primary tubes, but in the specimen used for illustration the external openings of the fifth and sixth tubes had fused to form a single pore, there thus being but eight surface pores along the line. In an adult specimen of *Polypterus ornatipinnis* this anastomosis of these two pores had not taken place, and there were accordingly nine primary pores related to the line. In the specimen used for fig. 30, there were four nerves entering the canal as it traversed the preoperculum, but whether there were three or four sensory organs was not determined.

The lateral line of the body begins posterior to the posttemporal bone, and is represented by longitudinal grooves on the external surfaces of successive scales, the grooves on the first seven rows of scales forming three short lines, the first one of which lies in the line of the hind end of the cranial canal, the next one slightly ventral to the first one, and the third one still farther ventrally. The next groove lies slightly ventral to the third short line, and from there the line of grooves continues in an unbroken line to the base of the tail fin, there being one groove on each successive scale. Dorsal to this line, approximately in the line of the dorso-anterior one of the three short lines, there is another line of sense organs, the positions of which are indicated by

a somewhat irregular line of grooves placed transversely on every third or fourth scale; and dorsal to this line there is, along the ventral edge of the dorsal fin, a line of short longitudinal grooves, approximately one on each successive scale.

On the head there are six short lines of surface organs, each marked by a slight depression on the external surface of the underlying bone: an anterior head-line on the dorsal surface of the frontal, mesial, or postero-mesial to pore 6 supraorbital; a middle head-line on the parieto-dermopterotic, mesial, or postero-mesial to pore 11 infraorbital; an anterior horizontal cheek-line on the cheek-plate somewhat posterior to pore 8 infraorbital; a posterior horizontal cheek-line on the cheek-plate immediately anterior to pore 8 preoperculo-mandibular; a vertical cheek-line on the cheek-plate immediately ventral to the posterior horizontal cheek-line; and a transverse line on the ventral surface of the gular plate.

Myology

Eye muscles. The recti superior, inferior and externus arise from a short tendinous stalk that has its origin on the sphenoid, near its ventral edge and immediately posterior to the foramen opticum, its position and its relation to these muscles suggesting the eye stalk of the Selachii. The rectus internus has its origin directly upon the sphenoid, near its ventral edge and anterior to the foramen opticum, between that foramen and the foramen for the orbito-nasal artery. The obliquus superior arises from the ectethmoid, on the edge of, and partly within, the preorbital canal, the obliquus inferior arising from that same bone, near its ventral edge.

The innervation of these muscles is as in Amia (Allis, 1897), excepting in that the inferior division of the nervus oculomotorius passes dorsal, instead of ventral, to the rectus inferior.

Muscles innervated by the nervus trigeminus. These muscles have been described by both Pollard (1892) and Luther (1913).

The musculus adductor mandibulae, the masseter of Pollard's and Luther's descriptions, has, in my adult specimens, the superficial (upper) and deeper (lower) portions described by Pollard but not found by Luther. In the 75 mm. specimen both portions are also found, but not so distinctly separated from each other as in the adult. The superficial portion is the larger, and has its origin in part on a line of tough connective tissue that is attached to the internal surface of the dorsal border of the cheek-plate, in part on the external surface of the dorsal portion of the hyomandibula, and in part on the external surface of that part of the palatoquadrate that lies posterior to the ridge that runs upward across the quadrate from the outer end of its articular edge. The dorsal edge of the muscle is thin, and along a part of this edge is the line of tough connective tissue, above referred to, which is firmly attached to the dorsal edge of the cheek-plate and hence serves in part as surface of origin of the muscle, and in the 75 mm. specimen this is the only origin that the muscle has. The surface of origin on the palatoquadrate covers

parts of the quadrate, entopterygoid and metapterygoid, and that on the hyomandibula the anterior portion of that bone from the dorsal edge of the palatoquadrate upward to the line of the opercular process, the fibres of the muscle all having their origins on a tough membrane that covers these several bones, and not directly on the bones themselves. A slip of that part of the membrane that covers the surface of origin on the palatoquadrate extends posteriorly, external to the ramus mandibularis facialis, and is inserted on the hyomandibula posterior to that nerve (fig. 46). The fibres of the muscle converge toward the ascending process of the splenial, running antero-ventrally, anteriorly, and even antero-dorsally, and the dorsal and larger part of them are inserted on the dorsal edge of that process and along the internal surface of its hind edge, the ventral fibres passing directly into the ramus of the mandible and there being inserted on the internal surface of the dermarticular.

The deeper portion of the adductor arises from that part of the quadrate that lies anterior to the ridge that runs upward from the outer end of its articular edge, these fibres, like those of the superficial portion of the muscle, arising from a membrane that covers the quadrate and not directly from that bone. The fibres of this portion of the muscle run antero-ventrally and are inserted, mostly tendinous, on the internal surface of the dermarticular, the tendinous ends of the muscle passing mesial, or in part lateral and in part mesial, to the ramus mandibularis trigemini. Associated with this part of the adductor there is a short muscle which corresponds to the mandibular portion of the muscle of Amia and certain of the Teleostei. The fibres of this latter muscle arise from the stout flat tendon of the musculi temporalis and pterygoideus, to be described below, and running ventro-anteriorly are inserted on the dorsal surface of the hind end of Meckel's cartilage.

The musculus temporalis has its origin from the ventral surface of the postfronto-sphenotic, from the supraorbital band of cartilage, and from that part of the ventral surface of the frontal that roofs the supraorbital fontanelle, the surface of origin of the muscle extending forward to the transverse plane of the foramen opticum. From this long surface of origin, the fibres of the muscle run postero-ventrally, ventrally and antero-ventrally, and passing external to the rami ophthalmicus profundus and ophthalmicus superficialis trigemini, and internal to the rami maxillaris and buccalis trigemini, are all inserted on the external surface of a tendinous band which lies between it and the musculus pterygoideus and which gives insertion, on its internal surface, to the fibres of the latter muscle. This tendinous band passes internal to the ramus mandibularis trigemini and, diminishing in width, is inserted on the internal surface of the dermarticular.

The musculus pterygoideus arises from the postero-ventral portion of the lateral surface of the sphenoid and from adjacent portions of the mesial plate of the ascending process of the parasphenoid, there lying between the nervus trigeminus dorsally and the common carotid artery, the ramus palatinus

facialis, and the vena orbitalis inferior ventrally. It is a wide stout muscle, runs ventro-laterally and slightly anteriorly along the external surface of the palatoquadrate, and has its insertion on the tendinous band, just above described, that gives insertion on its external surface to the musculus temporalis.

The musculi temporalis and pterygoideus apparently together correspond to the first and second divisions of the levator maxillae superioris of my descriptions of Amia (Allis, 1897).

The single primitive levator arcus palatini has been more or less completely differentiated into four muscles; the levator arcus palatini of Luther's descriptions (levator maxillae superioris of Pollard), the protractor hyomandibularis of Pollard's descriptions, the dilatator operculi, and the musculus spiracularis (Luther). These muscles, excepting the spiracularis, all arise together from the lateral surface of the postfronto-sphenotic, there forming practically a single muscle but separated from each other by an aponeurotic formation. The fibres of the levator arcus palatini run postero-ventrally and, spreading somewhat, are inserted on a curved tendinous band which is concave postero-ventrally. This band crosses the external surface of the protractor hyomandibularis at about the middle of its length, and has its ventro-anterior end inserted on the dorsal edge of the entopterygoid, and its dorso-posterior end on the external surface of the hyomandibula in the horizontal line of its opercular process. The dilatator operculi lies along the dorsal edge of the levator arcus palatini, and runs posteriorly and slightly laterally. Its fibres are all inserted on a long tendinous formation which extends the full length of the muscle, along the middle line of its external surface, and has its insertion on the internal surface of the anterior edge of the operculum. The musculus spiracularis lies along the dorsal edge of the dilatator operculi, and in the adult has its origin on the hind edge of the frontal bone, as Luther states. Pollard calls it a slip of the dilatator, but even in my 75 mm. specimen it is wholly independent of that muscle. It runs posteriorly along the lateral edge of the spiracular opening, and apparently has its insertion on the wall of that opening. It lies directly beneath the spiracular ossicles and is attached to them by fibrous tissues, but not inserted on them. The protractor hyomandibularis lies internal to the levator arcus palatini, and is a much stouter muscle. Its fibres run postero-ventrally and most of them are inserted on a membrane that covers and forms part of the lateral wall of the spiracular canal, that membrane having its attachment, ventrally, to the dorsal edge of the palatoquadrate and, posteriorly, to the anterior edge of the hyomandibula, the longest fibres of the muscle, which are the external ones, only extending to the edges of those two skeletal elements and not overlapping them. The muscle thus has an action upon the suspensorial apparatus that is strictly similar to that of the so-called levator arcus palatini, and, in addition, an action of some sort on the spiracular canal.

There is no muscle comparable to the intermandibularis of Amia, but

there are two muscles strictly comparable to the geniohyoidei inferior and superior of that fish, and I have described them in an earlier work (Allis, 1919*d*). The geniohyoidei inferior and superior of this fish are called by Pollard the intermaxillares anterior and posterior, the former being said to be innervated by the ramus mandibularis trigemini and the latter by the ramus hyoideus facialis. Holmqvist (1910) calls the anterior one of these two muscles the intermandibularis, and the posterior one the protractor hyoidei, and he says that the latter muscle, as an independent structure, is found only in the bony fishes and in Amia, the term bony fishes, as employed by him, evidently meaning the Teleostei only. In a later work (1911), Holmqvist calls the intermandibularis of his earlier descriptions of Polypterus the intermandibularis II, in order to distinguish it from an intermandibularis such as is found in Amia, which latter muscle is called the intermandibularis I; and these two muscles, where found, are both considered by him to be innervated by the ramus mandibularis trigemini. The protractor hyoidei, which is the geniohyoideus superior of my descriptions of Amia, is, on the contrary, considered by him to be innervated by the ramus hyoideus facialis. In the Teleostei the homologue of this latter muscle of Polypterus is said (1910, p. 12) to have added to it certain fibres derived from the constrictor of the mandibular arch, the anterior portion of the muscle then being innervated by the nervus trigeminus and its posterior portion by the nervus facialis. It is said that, in both Polypterus and Lepidosteus, none, or but few, of these trigeminus fibres have as yet been acquired by the protractor, and Holmqvist's descriptions would seem to indicate that he did not consider them, where found, to have been derived from the intermandibularis II (geniohyoideus inferior). Where they are considered to have come from is not clear. Luther (1913), following Holmqvist's earlier work, calls the two muscles of Polypterus the intermandibularis and protractor hyoidei, and he says that the former muscle is derived from the ventral portion of the constrictor of the mandibular arch, and is innervated by the ramus mandibularis trigemini, while the protractor hyoidei is derived from the ventral portion of the constrictor of the hyal arch and is innervated by the ramus hyoideus facialis.

The contraction of either of these two muscles would evidently have similar effect upon either the mandible or the hyal arch, and in my work on Amia, I said (Allis, 1897, p. 562) that this action must be either that of an adductor (more properly protractor) of the hyal arch or a retractor of the mandible, according as the one or the other of these two structures was fixed and stationary. If then the principal action of the posterior muscle is that of a protractor hyoidei, as Holmqvist's descriptions would seem to establish, that must be the action also of the anterior muscle. The two muscles, in fact, become, in certain of the Teleostei described by Holmqvist, simply anterior and posterior portions of a single muscle, but apparently always separated from each other by a more or less developed aponeurotic line. If one of them is called a protractor hyoidei, the other should then also be so called, one being

an anterior protractor and the other a posterior one. I have however thought best, for the sake of conformity in my several works, to continue to use for them the names employed in my descriptions of Amia and Scomber.

The geniohyoideus inferior, thus defined, is a muscle strictly similar to that of Amia, arising in the median line from a median aponeurotic raphe common to it and its fellow of the opposite side, and running antero-laterally to be inserted mainly upon the mesial surface of Meckel's cartilage, immediately ventral to the ventral edge of the splenial, but partly also along the ventral edge of the latter bone. The geniohyoideus superior arises, as in Amia, from the proximal (posterior) end of the ceratohyal, and, running anteriorly and somewhat mesially, has its mesial fibres inserted on a posterior continuation of the median raphe that gives insertion to the geniohyoideus inferior, while the lateral fibres pass internal (dorsal) to the geniohyoideus inferior and are inserted on the dorsal portion of the raphe that gives insertion to the fibres of that muscle. The fold of the mucous membrane of the mouth cavity that lies beneath the tongue, lies between the lateral portions of the two geniohyoidei.

The mesial edge of the geniohyoideus superior is in contact with the lateral edge of the hyohyoideus inferior, the two muscles there forming a single and practically continuous sheet. The two muscles are however certainly innervated, as fully explained in my recent work (Allis, 1919*d*), the one by the nervus trigeminus, and the other by the nervus facialis, and the fibres of the one pass ventral, and those of the other dorsal, to a fold of the dermal tissues that extends inward between the two muscles and spreads laterally on either side, thus forming a short fold, or pocket, between the two muscles. This pocket opens, superficially, into a long and narrow median space formed by the infolding of the dermis inward and laterally beneath the mesial edge of each gular plate, this space extending anteriorly nearly to the anterior edge of the geniohyoideus inferior.

Muscles innervated by the nervus facialis. The adductor hyomandibularis and adductor operculi, called by Pollard the retractor hyomandibularis and the opercularis, form a single continuous muscle which has its origin on the large concave surface on the dorso-lateral surface of the posterior portion of the opisthotic ridge, and the anterior portion of the muscle is inserted on the internal surface of the hyomandibula and the posterior portion on the internal surface of the operculum.

The hyohyoideus has inferior and superior portions similar to those of Amia, the inferior portion being called by Pollard both the mantle muscle and the muscle of the jugular plate. Of it he says: "Behind the intermaxillaris is a separate muscle which arises from a median raphe of its own, and proceeds to the postero-internal angle of the jugular plate. Some fibres pass on into the mantle." Starting from this median aponeurotic raphe, which is common to it and its fellow of the opposite side and lies internal to the raphe of the geniohyoidei, the muscle runs posteriorly in the gill cover and becomes a wide

thin sheet the lateral edge of which is contiguous with the mesial edge of the geniohyoideus superior, as already explained. Slightly posterior to the hind end of the latter muscle, the hyohyoideus ends as a continuous muscle sheet, but separate bundles are continued onward in the gill cover and form the hyohyoideus superior. No fibres of either division of the muscle have any attachment to the gular plate. The hyohyoideus superior continues upward in the gill cover, as a series of small and somewhat stringy muscle bundles, the anterior bundles all ending at the ventral edge of the operculum, but the posterior ones extending the full length of the gill cover, as shown in fig. 45. In my 75 mm. specimen certain bundles of these fibres have undergone specialisation in relation to the external gill, and form a relatively large muscle which lies ventral to the external gill and sends branches into it. The hind end of the ventral edge of the adductor operculi lies dorsal to the external gill, and doubtless also acts upon it, the base of the gill lying between it and the large bundle of the hyohyoideus above referred to.

Muscles innervated by the nervi glossopharyngeus and vagus. The levator muscle of the first branchial arch arises by two independent heads, one of which has its origin on the opisthotic ridge immediately dorsal to the foramen faciale and the other on the lateral plate of the ascending process of the parasphenoid ventral to the latter foramen. The truncus hyomandibularis facialis and the efferent artery of the hyal arch pass between these two heads, the one to enter the jugular canal and the other the canalis parabasalis. Beyond this nerve and artery the two heads of the muscle unite to form a single muscle, which runs postero-ventrally and has its insertion in part on the pharyngobranchial of the first branchial arch and in part on the epibranchial of that arch. The stout ligament that extends from the ventro-postero-lateral corner of the ascending process of the parasphenoid to the dorsal end of the ceratobranchial of the first branchial arch passes across the external surface of that part of the muscle that is inserted on the pharyngobranchial.

Posterior to this muscle there are four levator muscles, all of which have their origins on the large concave surface on the dorso-lateral aspect of the posterior portion of the opisthotic ridge, their surfaces of origin lying ventral to those of the adductores hyomandibularis and operculi. The levatores all run postero-ventrally, each one overlapping externally, to a considerable extent, the next posterior muscle. The levators of the second and third branchial arches are each inserted on the epi-pharyngobranchial of their arch, the levator of the fourth arch being inserted on the dorsal end of the ceratobranchial of its arch. Wiedersheim (1904) says that this latter levator is in large part inserted on a tendinous line which separates it from part of the transversus ventralis, but it was not so found in my specimens. The fifth, and last levator is inserted on the anterior edge of the clavicle, and varies considerably in importance in different specimens, being wholly wanting in certain of them. The first four levators are each innervated by a branch of the nerve of its arch. The innervation of the fifth levator was not determined in the

one fish examined in which the muscle was well developed. In a second fish, in which the muscle had the appearance of being a small slip of the fourth levator, it was innervated by a branch of the nerve of that arch. It represents the musculus trapezius of the Plagiostomi (Allis, 1917). The dorsal end of the clavicle is enclosed in a sheath-like formation of connective tissue, and certain fibres of the trunk muscles, inserted on it, have somewhat the appearance of a rudimentary trapezius, but they do not represent that muscle.

There are, as Pollard states, no interarcuales dorsales and no adductores arcuum branchialium.

The interarcualis ventralis of the first branchial arch arises from the ventral surface of the ceratobranchial of its arch, near its distal end, and running almost directly forward is inserted, by tendon, on the dorsal surface of the ceratohyal, near its distal end.

The interarcualis ventralis of the second branchial arch is somewhat separated, at its origin, into two parts. One of these parts forms the postero-mesial portion of the entire muscle and has its origin immediately distal to the little process, capped with cartilage, near the distal end of the ceratobranchial of its arch. The other part forms a wide muscle-sheet which has its origin partly on the distal end of the ceratobranchial and partly on the hypobranchial of the arch, but mostly on a ligamentous band which has its origin on the ceratobranchial of the first arch and from there extends postero-mesially and is in part inserted on the second arch, and in part either passes between the two parts of the interarcualis of that arch, or passes ventral to both of them, and reaches the ventral wall of the pericardial chamber, where it continues onward in that wall and, entering the tough connective tissue that lies between the two sternohyoidei, is inserted on the clavicle. From these several surfaces of origin, the fibres of the muscle run anteriorly and antero-mesially and are all inserted on a ligamentous band which is attached, anteriorly, to the dorsal edge of the distal end of the ceratohyal, contiguous to and continuous with the tendon of the interarcualis of the first arch. From there the band extends postero-mesially dorsal to the afferent arteries of the hyal and first branchial arches, and, posterior to the common trunk of those two arteries, turns mesially ventral to the truncus arteriosus and is continuous with its fellow of the opposite side.

The interarcualis ventralis of the third arch has its origin on the ceratobranchial of its arch immediately distal to the little process, capped with cartilage, near the distal end of that element. It lies internal (dorsal) to the interarcualis of the fourth arch, and is largely concealed from view until that muscle is removed. It runs antero-mesially and is inserted on the lateral edge of the posterior, cartilaginous portion of the large basibranchial. It is innervated by branches of the nerve of its arch.

The interarcualis ventralis of the fourth arch has its origin on the ceratobranchial of its arch, dorsal to that distal portion of the bone that corresponds to the hypobranchials of the more anterior arches. Running forward and but

slightly mesially, ventral and hence superficial to the interarcualis of the third arch, it is inserted on the ligamentous formation that serves as surface of origin for the anterior portion of the interarcualis of the second arch. It is innervated by the nerve of its arch, and not by the nervus hypoglossus, as Pollard thought probable.

The pharyngo-clavicularis is, at its origin, a single continuous muscle which arises from the anterior edge of the ventral portion of the clavicle. It runs almost directly forward, but slightly dorsally and mesially, and separates into two parts which are inserted, one on that part of the fourth ceratobranchial that corresponds to the ceratobranchial of the more anterior arches and the other on the part that corresponds to the hypobranchial, the two parts straddling the afferent artery of the arch. In *Polypterus ornatipinnis* the muscle fibres are inserted directly on the ceratobranchial. In *Polypterus bichir* the two parts each become tendinous and the tendons are inserted on the ceratobranchial at a considerable distance from each other. The muscle is innervated by branches of the pharyngeal branch of the nervus vagus, as stated in one of my earlier works (Allis, 1917, p. 358). This muscle is not described by Pollard.

The transversus ventralis is a large muscle-sheet which arises, on either side, from the fourth ceratobranchial and has its insertion in a median aponeurotic raphe common to it and its fellow of the opposite side, as Pollard states. It lies directly internal (dorsal) to the pericardial chamber, and is continuous, posteriorly, with the constrictor oesophagei. It is innervated by branches of the pharyngeal branch of the nervus vagus. Wiedersheim (1904) calls it the constrictor pharyngis, and says that its anterior portion is an adductor of the fourth branchial arches.

Longitudinal ventral muscles. There are but two of these muscles, the sternohyoideus and branchiomandibularis.

The sternohyoideus, called by Pollard (1892) the coracohyoideus, has its origin on the dorso-anterior surface of the ventral portion of the clavicle. It is a stout muscle crossed by two aponeurotic septa which extend entirely through it. It ends anteriorly in a stout tendon which passes dorsal to the afferent arteries of the hyal and first branchial arches and is inserted mainly on the hypohyal, but partly also in the tough connective tissues that cover the ventral surface of the tongue. The tendon of the muscle encloses, near its mesial edge, a small bone, and a slender median Y-shaped bone lies between the muscles of opposite sides, enclosed in tough connective tissue that lies between the muscles near their dorsal surfaces. This tough tissue is attached to the ventral surface of the pericardial chamber and encloses the two ligaments, one on either side and already described, that have their origins on the ventral ends of the ceratobranchials of the first and second branchial arches.

The branchiomandibularis, called by Pollard the "branchiomandibularis sui geniohyoideus," arises mostly from the distal end of that part of the third

hypobranchial that forms the ventral one of the two heads by which it articulates with the basibranchial, but certain of its fibres have their origins on the anterior wall of the pericardial chamber. It runs at first ventro-antero-mesially and passes, with its fellow of the opposite side, between the basal portions of the tendons of the sternohyoidei, the two branchiomandibulares there being closely pressed together. The muscle then passes ventral to the afferent arteries of the hyal and first branchial arches, and, spreading somewhat, runs directly forward, dorsal (internal) to the hyohyoideus inferior and to both divisions of the geniohyoideus, and is inserted on the dentary close to the symphysis. Near their insertions, the muscles of opposite sides are separated by a tough median septum of fibrous tissue which spreads laterally, on either side, both dorsal and ventral to the muscles, there lying between them and the adjacent portions of the external epidermis and the lining membrane of the mouth cavity.

The muscle is innervated by a branch of the spino-occipital nerves.

Angiology

Vena jugularis. The vena jugularis of Polypterus is formed by the union of two veins, one of which is supraorbital and the other infraorbital in position. The former corresponds to the orbito-nasal vein of Allen's (1905) descriptions of the mail-cheeked fishes, but as it closely accompanies the ophthalmic artery and the ramus ophthalmicus superficialis trigemini it may be called the ophthalmic vein. The infraorbital vein closely accompanies the orbito-nasal artery, and it might, accordingly, be called the orbito-nasal vein, but to avoid confusion it seems best to call it simply the infraorbital vein. It apparently has no homologue in Allen's descriptions, for the vein called by him the facialis-maxillaris is said to accompany the ramus maxillaris trigemini in the posterior portion of its course through the orbit. These veins and their several branches were traced in the 75 mm. specimen, and not in the adult, and the following descriptions relate to them as there found.

The ophthalmic vein has its origin in numerous little branches on the dorsal surface of the anterior end of the snout, some of these branches running posteriorly along the dorsal surface of the nasal capsule and others entering that capsule through the fenestra nasalis. These latter branches unite to form a single vein which runs posteriorly along the dorsal surface of the nasal sac, between it and the roof of the nasal capsule, there being accompanied by a branch of the ophthalmic artery, a branch of the ramus ophthalmicus profundus, and the terminal portion of the ramus ophthalmicus superficialis trigemini, the latter nerve containing the latero-sensory fibres that innervate the sense organs in the os terminale and the accessory nasal bone. While in this position the vein receives one large, and possibly other smaller branches coming from the nasal sac, and the vein so formed, together with the accompanying nerves and artery, perforates the roof of the nasal capsule and issues at the anterior end of a groove on its dorsal surface. This groove is short,

leads posteriorly into the preorbital foramen, and through that foramen into the dorso-anterior portion of the orbit. While in this short groove the vein receives a vein formed by the fusion of the branches, above referred to, that arise on the anterior end of the snout and run posteriorly along the external surface of the nasal capsule, and the so-formed vein then traverses the foramen preorbitalis and enters the orbit along with the accompanying nerves and artery.

The short groove above described is shown in the accompanying fig. 10, of the chondrocranium of the adult; is shown in Pollard's figure giving a dorsal view of the chondrocranium of his 21 cm. specimen of Polypterus; is apparently shown in Budgett's figure of his 30 mm. larva as a slit-like opening that lies immediately anterior to the preorbital foramen; and is described by Lehn (1918, p. 388) as a large opening (grosse Öffnung) which leads into a canal which opens into the orbit and is considered by her to be an anterior eye-muscle canal. Pollard shows a foramen at the anterior end of the groove and calls it the canalis ethmoidalis, this name seeming to indicate that he here found a canal and that he considered it to be the homologue of the similarly named canal in Gegenbaur's (1872) descriptions of the Selachii. There is no canal here in my 75 mm. specimen, but conditions found in the adult indicate that the anterior end of the groove might become roofed by cartilage and so be converted into a short canal. This canal would, however, not be the homologue of the canalis ethmoidalis of Gegenbaur's descriptions of the Selachii, for that canal simply traverses the cartilage of the nasal capsule from its dorsal to its ventro-lateral surface without at any point entering or communicating with the cavity of the capsule. In Heptanchus I find this canal traversed by an important vein which connects the ophthalmic and infra-orbital veins, but the canal is not traversed either by the ophthalmic artery or by the lateralis branches of the ophthalmicus superficialis trigemini, these latter structures running forward on the dorsal surface of the nasal capsule without at any point perforating it. The canal of Heptanchus and the groove or canal of Polypterus are thus not homologous, and I have accordingly called the groove of Polypterus the antero-mesial ethmoidal groove, to distinguish it from the postero-laterally situated canal of Heptanchus.

Having entered the orbit, the ophthalmic vein runs posteriorly in its dorsal portion and, in the 75 mm. specimen, receives several branches: one from the musculus obliquus superior; two from the dorsal surface of the cranium through foramina that perforate the roof of the orbit; two from the cranial cavity, each branch issuing through an independent foramen in the cartilaginous portion of the orbital wall; a branch formed by the fusion of one vein coming from the musculus rectus superior and another from the eyeball, accompanying the nervus ciliaris longus; a branch from the temporal and pterygoid divisions of the musculus adductor mandibulae; and one that is formed by branches from the masseter division of the adductor, from the levator maxillae superioris, and from the mandible. The latter one of these

several branches is evidently the mandibular vein, for it is the only branch from the mandible that reaches the jugular vein. It accompanies, in its course, the ramus mandibularis trigemini, and receives a branch that accompanies the ramus maxillaris trigemini. It is accordingly a maxillo-mandibular vein, and will be so referred to.

After receiving these several branches, the ophthalmic vein has become what I wrongly called, in an earlier work (Allis, 1908*b*), the external jugular, and the posterior one of the two branches received from the cranial cavity was there said to probably be the encephalic vein of Allen's (1905) descriptions of the Loricati. In favour of the latter assumption is the fact that the vein receives branches from the region of the hypophysis, but, as noted in my earlier work, its foramen of exit has a markedly different position from that of the encephalic vein of the Loricati.

The ophthalmic vein, in its course through the orbit, lies along the mesial wall of the orbit, internal to the musculus temporalis and dorsal to the nervi opticus, oculomotorius and profundus. When it reaches the hind end of the orbit it lies beneath the overhanging anterior portion of the postorbital process, and there passes between the ganglia formed on the lateralis-communis and general sensory-motor roots of the nervus trigeminus, ventral to the former and dorsal to the latter. These ganglia are both extracranial in position, and they and the ophthalmic vein all lie beneath the overhanging postorbital process, that process here enclosing the dorso-anterior portion of the anterior semicircular canal. Posterior to this, the vein and ganglia lie in a recess in the cranial wall, closed externally by the lateral plate of the ascending process of the parasphenoid, the chamber so formed being "the trigeminus portion of a perfectly typical trigemino-facialis chamber" (Allis, 1908*b*, p. 220), and strictly similar to the trigemino-facialis chamber of Stensiö's (1921) descriptions of *Birgeria mougeoti*. The general sensory-motor root of the trigeminus now soon perforates the mesial wall of this chamber, its foramen lying, in the adult, at the bottom of a small but marked recess on the cerebral surface of the cranial wall. Posterior to this, the lateralis-communis root traverses the cranial wall through a short canal which opens into the anterior end of the labyrinth recess, the ophthalmic vein continuing posteriorly external to the cranial wall and dorsal to the general sensory-motor root, and being joined, posterior to the latter root, by the infraorbital vein to form the vena jugularis.

The infraorbital vein arises in the tissues at the anterior end of the snout, and runs posteriorly along the ventral surface of the nasal capsule, no branches, so far as could be traced, entering the nasal capsule and running posteriorly between that capsule and the nasal sac, as is the case with the ophthalmic vein. Near the hind end of the nasal capsule it receives a large branch from the nasal sac, and another from the labial fold. The branch from the nasal sac traverses a foramen in the floor of the nasal capsule together with a branch of the maxillary artery and a branch of the ramus maxillaris trigemini, and in the nasal sac it forms anastomoses both with the ophthalmic vein and with

a vein that comes from the cranial cavity through the foramen olfactorium. The infraorbital and ophthalmic veins are thus here connected with each other, but this connection is by branches that traverse the nasal sac, instead of, as in the Selachii, by a branch that passes outside the nasal capsule.

The infraorbital vein, after receiving these two branches, runs posteriorly along the floor of the orbit, receiving branches from the maxillary region, from the musculi obliquus inferior, rectus internus, rectus inferior and rectus externus, and one from the eyeball that accompanies the nervus ciliaris brevis. Close to this latter vein it apparently receives a branch that comes from the large orbital lymph sinus, that sinus also apparently being connected with that branch of the ophthalmic vein that accompanies the nervus ciliaris longus. The infraorbital vein here lies ventral to the musculus pterygoideus, along the lateral edge of the parasphenoid and immediately dorsal to the common carotid artery, and when it reaches the hind end of the orbit, it passes dorsal to the anterior edge of the horizontal plate of the ascending process of the parasphenoid, and, lying in the angle between that plate and the mesial plate of the process, receives the pituitary vein, which issues from the pituitary fossa through the pituitary foramen. The infraorbital vein then runs upward posterior to the general sensory-motor root and ganglion of the trigeminus, and falls into the ophthalmic vein, as above described.

From this description of these two veins it is evident that, in this fish, the basal portion of the vena ophthalmica is formed by that portion of the vena capitis lateralis that lies anterior to the nervus facialis, and the vena infraorbitalis by the corresponding portion of the vena capitis media plus the posttrigeminus commissure between that vein and the vena capitis lateralis. The conditions seem to indicate that a pretrigeminus commissure between the venae capitis media and lateralis primarily existed, and that the vena maxillo-mandibularis acquired connection with it. The commissure then lost its connection with the vena capitis media, but retained that with the vena capitis lateralis and so became the basal portion of the vena maxillo-mandibularis. The vena infraorbitalis retained its connection with the primitive vein (cardinalis anterior), as did also the pituitary vein. This would fully explain the conditions actually found, and the vena jugularis, instead of beginning anterior and ventral to the nervus trigeminus, begins posterior and dorsal to it, this being, so far as I know, exceptional in fishes, and an excellent example of how difficult it is to give names to these veins of fishes that will definitely indicate their homologies.

The vena jugularis, formed, as above set forth, by the union of the ophthalmic and infraorbital veins, at first lies internal to that portion of the lateral plate of the ascending process of the parasphenoid that lies dorsoanterior to the line of fusion with the mesial plate of that process, and then enters that short canal in the cartilaginous side wall of the cranium that has been already referred to as the jugular canal. Posterior to the anterior opening of this jugular canal, the lateral and mesial plates of the ascending

process of the parasphenoid fuse with each other, and the projecting dorsal end of the so-formed plate lies against the outer wall of the jugular canal. The jugular vein is accompanied, as it enters its canal, by the ramus palatinus facialis and a general sensory branch sent from the trigeminus ganglion to the truncus hyomandibularis facialis. The ramus palatinus facialis soon falls into the communis root of the nervus facialis, that root perforating the mesial wall of the jugular canal along with the lateralis and motor roots of the nerve. This foramen is thus the foramen primitivum faciale, and it lies ventral to the vena jugularis. Shortly posterior to this foramen, the jugular canal opens on the external surface of the chondrocranium, but it is still, for a few sections, closed externally by the fused dorsal ends of the mesial and lateral plates of the ascending process of the parasphenoid. The mesial plate of the ascending process then vanishes in the sections, and the vein and the nervus hyomandibularis facialis lie in a groove in the cartilaginous lateral wall of the cranium, still enclosed externally, for a short distance, by the hind edge of the lateral plate of the process. The posterior opening of the jugular canal is accordingly the foramen faciale of the skull of the adult. Posterior to this foramen the vein lies in the jugular groove on the lateral surface of the cranium, and there receives venous vessels from the hyal and each of the branchial arches, and also the vena jugularis interna, which issues from the cranial cavity through the foramen vagum.

Afferent and efferent arteries. The truncus arteriosus (figs. 51–54) gives off, immediately after issuing from the pericardial chamber, a large vessel on either side which runs laterally anterior to the musculus branchiomandibularis, at its point of origin, and immediately separates into two parts, one ventral to the other, which are, respectively, the afferent artery of the second branchial arch and the united trunks of the afferent arteries of the third and fourth arches.

The afferent artery of the second branchial arch runs outward internal (dorsal) to the interarcualis ventralis of the fourth arch, and posterior both to the head of the hypobranchial of its own arch and to the interarcualis ventralis, and reaches the ventral surface of the ceratobranchial of its arch.

The trunk formed by the united afferent arteries of the third and fourth branchial arches turns posteriorly, passes between the two articular heads at the distal end of the third hypobranchial, then internal (dorsal) to the interarcualis ventralis of the third arch, at its insertion, and at the hind edge of that muscle separates into its two parts, the afferent arteries of the third and fourth arches. The afferent artery of the third arch turns laterally and reaches the ventral surface of the ceratobranchial of its arch. The afferent artery of the fourth arch continues posteriorly, passes across the dorsal (internal) surface of the fourth ceratobranchial, in the marked groove on that surface and between that bone and the related dermal plates, and turning dorso-laterally across the hind edge of the ceratobranchial, passes between the inferior and superior divisions of the musculus pharyngo-clavicularis and reaches the

ventral (external) surface of its ceratobranchial. This artery thus has the relations to the distal end of its ceratobranchial that the artery of the third arch has to the ventral one of the two articular heads at the distal end of its hypobranchial, which suggests that these parts of these two bones may be homologous, for otherwise it would be difficult to explain how the artery has come to twist completely around the branchial bar of its arch in order to reach its ventral (external) surface.

After giving off this large branch on either side, the truncus arteriosus continues forward, and approximately in the level of the articular head of the hypobranchial of the first arch gives off a large branch on either side and then continues onward as a small and unimportant median artery which could be traced a short distance in the adult, but was not even evident in the 75 mm. specimen. The large branch on either side lies dorsal (internal) to the musculus branchiomandibularis, and soon separates into the afferent arteries of the hyal and first branchial arches. The latter (fig. 52) runs laterally across the ventral surface of the tendon of the musculus sternohyoideus and ventral to the interarcualis of its arch, and reaches the ventral surface of the ceratobranchial of its arch. The afferent hyal artery runs posteriorly along the ventral surface of the musculus sternohyoideus and reaches the ventro-mesial edge of the ceratohyal, near its proximal end, where it turns dorso-laterally along the posterior surface of the epihyal and the corresponding edge of the hyomandibula, and becomes the efferent artery of the arch.

The median dorsal aorta, running forward, reaches the hind end of the cranium, and there enters the aortic canal in the basis cranii. Running forward in that canal it separates into its two branches, the lateral dorsal aortae, each of which issues from the aortic canal into the canalis parabasalis in the ascending process of the parasphenoid. Immediately before entering the aortic canal, the dorsal aorta receives the efferent artery of the second branchial arch, and immediately posterior to that artery the efferent arteries of the third and fourth branchial arches, these two latter arteries usually being fused to form a single trunk. Posterior to these several arteries the dorsal aorta gives off a single artery which runs posteriorly beyond the head region and was not traced, and then the subclavian arteries. Immediately after issuing from the aortic canal, the lateral dorsal aorta of either side receives, close together, the efferent arteries of the hyal and first branchial arches, and then continues onward as the common carotid.

The afferent and efferent arteries of the branchial arches all lie between the two rows of branchial rays of their respective arches, the efferent artery lying internal to the afferent artery and each of them receiving, at the level of the dorsal end of the ceratobranchial, a relatively large branch which comes from those branchiae that lie dorsal to this point. The efferent artery of the hyal arch comes upward along the hind edge of the hyomandibula, and passes, with the ramus hyoideus facialis, between the hyomandibula and the ligament that extends from its opercular process to the accessory hyomandibula.

The efferent arteries were not farther traced in the adult, but in the 75 mm. specimen the artery of each of the first three branchial arches falls, at the ventral end of its arch, into a ventral longitudinal commissure which lies internal to all the afferent arteries and hence is an internal lateral hypobranchial artery (Allis, 1912). The efferent artery of the fourth arch does not fall into this commissure, but the subclavian artery does, this latter artery being, in fact, a direct posterior continuation of the commissure. From the efferent artery of the fourth arch a large branch is given off near the proximal end of the ceratobranchial of the arch, and sends branches to the oesophagus, to the air-bladder and to the heart. Between the roots of the second and third afferent branchial arteries, the lateral hypobranchial receives a small branch from the truncus arteriosus, and, continuing onward beyond the first efferent artery, passes internal to the afferent hyal artery and, turning mesially, enters the thyroid gland. There it separates into two parts, one of which continues mesially and joins its fellow of the opposite side, the other turning anteriorly and forming an anterior prolongation of the hypobranchial. The latter artery soon gives off two branches, one of which runs upward along the ventromesial (morphologically external) edge of the ceratohyal, and the other in similar relation to Meckel's cartilage, the former lying posterior to the ramus mandibularis internus facialis and the other anterior to that nerve. These two arteries are, the one the anterior efferent hyal artery and the other either the afferent mandibular artery, or the posterior efferent artery of that arch (Allis, 1916), and dorsal to the ramus mandibularis internus facialis they fuse with each other, and then immediately fall into a cross-commissural vein which extends from the efferent hyal artery to the mandibular branch of the carotid artery, the anterior portion of this commissure running forward along the external surface of the ventro-lateral edge of the palatoquadrate. Dorsal to the commissure the anterior efferent hyal artery continues upward, accompanies the ramus hyoideus facialis as it passes inward across the hind edge of the hyomandibula, and internal to the latter element falls into the epibranchial longitudinal commissure, described immediately below. Anterior to this artery a small artery arises from the cross-commissure and runs upward along the external surface of the palatoquadrate, between it and the overlying muscles, and apparently represents a dorsal continuation of the afferent mandibular artery.

Anterior to the afferent mandibular artery, the lateral hypobranchial artery continues onward, is joined by the terminal branches of the mandibular branch of the carotid, and then ends in a cross-commissural vessel which connects it with its fellow of the opposite side.

A dorsal, or epibranchial longitudinal commissure arises, in my 75 mm. specimen, by three roots, two from the median dorsal aorta before it enters the aortic canal, and one from the lateral dorsal aorta after it issues from that canal, a branch of this latter root going to the thymus.

Carotid arteries. The main branches of the carotid arteries were described

by me in 1908, and brief reference to them was made in a later work (Allis, 1916). In the work published in 1908, and also in a work published in that same year on the pseudobranchial and carotid arteries of Amiurus (Allis, 1908*a*), the descriptions are, in certain places, greatly confused, and I am unable to account for it excepting on the assumption that there was some resetting of the type after the proofs had been corrected. I was unfortunately absent from my laboratory at the time, and the proofs were corrected and returned by an assistant.

In my 75 mm. specimen the lateral dorsal aorta of either side issues from the aortic canal into the posterior portion of the canalis parabasalis, and there immediately receives the efferent arteries of the hyal and first branchial arches. It then becomes the common carotid, and runs forward in the canalis parabasalis accompanied by a lymph vessel, a sympathetic nerve, and a communicating branch from the nervus glossopharyngeus to the ramus palatinus facialis which would seem to represent, in this fish, Jacobson's anastomosis. No branch of the common carotid is sent into the jugular canal, but immediately anterior to the anterior opening of that canal a branch is sent upward posterior to the general sensory ganglion of the nervus trigeminus and then forward dorsal to that ganglion but ventral to the related lateralis-communis ganglion, this branch corresponding to the ophthalmic branch of the external carotid of Amia and the Teleostei. A branch is sent upward from this artery along the anterior surface of the spiracular canal, and other branches to the musculi pterygoideus, masseter, temporalis and obliquus superior, and to the dorsal surface of the head, the artery then traversing the foramen preorbitalis and accompanying the branches of the vena ophthalmica, as already described. Approximately in the transverse plane where this ophthalmic artery separates from the common carotid, the communicating branch from the nervus glossopharyngeus falls into the ramus palatinus facialis, the latter nerve then passing dorso-lateral, and hence posterior, to the ophthalmic artery.

After giving off this ophthalmic branch the remainder of the common carotid issues from the canalis parabasalis and then runs forward in the groove on the lateral edge of the body of the parasphenoid, accompanied by the lymph vessel that traverses the canalis parabasalis with it, and also by the ramus palatinus facialis, and when it reaches the hind edge of the foramen opticum it gives off the maxillo-mandibularis artery. That part of the carotid that lies between the latter artery and the ophthalmic artery thus contains both the internal carotid and a large part of the external carotid of the non-siluroid Teleostei, but, because of its position, so similar to that of the internal carotid of Amiurus (Allis, 1908*a*), it was given that name in my earlier work. It seems, however, better to consider it as still a part of the common carotid, the internal carotid being that part of the artery that remains after the maxillo-mandibular artery is given off.

The maxillo-mandibular artery runs ventro-laterally and soon separates into its maxillary and mandibular portions. The maxillary artery runs for-

ward through the orbit, giving off certain branches, and then traverses the foramen by which the nasal branch of the vena maxillaris issues from the nasal capsule. Inside that capsule a branch is sent into the nasal sac to join and fuse with a terminal branch of the orbito-nasal artery, the remainder of the artery running forward between the sac and the wall of the nasal capsule to issue through the fenestra nasalis. The mandibular artery runs ventrally and reaches a point that lies slightly posterior to the angle of the gape of the mouth, where it gives off a number of little branches which form the "much vasculated tissue" referred to in my earlier work (Allis, 1916, p. 116), one of these branches being the hyomandibular cross-commissural vessel there described. The mandibular artery then sends a branch into the labial fold, where it supplies both external and internal surfaces of the labial cartilage, and itself continues onward into the mandible and separates into two terminal branches, both of which fall into the lateral hypobranchial artery. The much vasculated tissue above referred to lies somewhat dorsal to the ventro-lateral edge of the palatoquadrate, and mesial to the bottom of the longitudinal groove on the dorsal surface of the buccal cavity that I have recently described as the secondary superior alveolo-labial furrow (Allis, 1919*c*).

The internal carotid artery, after it separates from the maxillo-mandibular artery, immediately gives off two branches, arising close together, one of which goes to the choroid gland and hence corresponds to the arteria ophthalmica magna of other fishes. The other branch is the posterior cerebral artery, which perforates the cranial wall immediately posterior to the nervus opticus and turns posteriorly in the cranial cavity, giving off as it traverses the cranial wall, a branch which goes to the eyeball and is apparently the arteria centralis retinae. The internal carotid artery then immediately gives off the anterior cerebral artery, which perforates the cranial wall between the posterior cerebral artery and the nervus opticus and supplies the anterior portion of the cranial cavity, a terminal branch traversing the foramen olfactorium and entering the nasal sac. The remainder of the artery is now the orbito-nasal artery, which continues onward, sends a branch to the choroid gland, another to accompany the ramus palatinus facialis and others to certain of the muscles of the eyeball, and then itself passes over the lateral edge of the cartilage of the basis cranii and penetrates the basal portion of the membranous lateral wall of the cranial cavity. Running forward in this membrane, it enters the cranial cavity, and then, always lying in, or external to the lining membrane of that cavity, and hence never entering the cavum cerebrale cranii, it reaches and enters the nasal capsule through the foramen olfactorium.

The internal carotid of my 75 mm. specimen of this fish, like that artery of Amiurus, thus passes lateral and then dorsal to the trabecula in order to enter the cranial cavity, instead of passing ventral and then mesial to the trabecula as it does in all other fishes that I know of.

Trigemino-facialis chamber. From the above descriptions of the veins,

arteries and nerves of this region, it is evident that the canal in the cranial wall traversed by the vena jugularis represents some part of a trigemino-facialis chamber, and it is probable that it represents the pars jugularis, and that part only of the posttrigeminus portion of the chamber. The pars ganglionaris of this part of the chamber must then be represented either in the short canal by which the nervus facialis traverses the cartilage of the cranium, or in some part of the anterior portion of the labyrinth recess. The trigeminus part of the chamber is represented in the space, between the lateral wall of the chondrocranium and the ascending process of the parasphenoid, that lodges both the trigeminus ganglion and the vena jugularis, and it would seem as if it must represent the entire chamber notwithstanding that it is not closed externally by cartilage. This condition of the chamber is apparently primitive, for it closely resembles that described by Stensiö in the Palaeoniscidae, as already stated.

Neurology

Nervus and lobus olfactorius. The nervus olfactorius of the adult is long, has a long intracranial course, and arises from a bulbus olfactorius that is separated from the remainder of the telencephalon by a slight constriction only, as Bing and Burckhardt (1905) have stated. The rhinocele extends about half the length of the bulbus.

In my 75 mm. specimen the nervus olfactorius is short, while the bulbus is relatively long, as it is shown to be in Bing and Burckhardt's figure of a 16·5 cm. specimen. The bulbus extends forward to the foramen olfactorium, and from its anterior end two bundles of fibres arise, one from its dorsal and the other from its ventral half, the dorsal half of the bulbus projecting forward slightly beyond the ventral one. These two bundles form the nervus olfactorius, which runs ventrally and but slightly antero-laterally, and enters the nasal capsule on the dorso-mesial aspect of its hind end. The bulbus is entirely separate from its fellow of the opposite side, but closely pressed against it, as far back as the line of attachment of the anterior edge of the tela choroidea.

There is, as shown in Bing and Burckhardt's figure of a median sagittal section of an 18 cm. specimen, a deep median fold in the tela choroidea, but the anterior end of the bottom of that fold, as there shown, lies at a much higher level than in my 75 mm. specimen, where it descends almost to the level of the floor of the third ventricle. The floor of the latter ventricle is here thin, and in the transverse plane of the foramen interventriculare rises slightly in the median line, so that it has, in transverse sections, the shape of an inverted V, the top of this inverted V meeting the bottom of the median fold of the tela. Anterior to this point there is, on either side, a tall and narrow anterior prolongation of the ventricle, which forms a sort of diverticulum extending through 10 sections of 15μ each. The dorsal end of each diverticulum is enlarged, and is prolonged anteriorly as a short projecting pocket which lies on the dorsal surface of the related bulbus. Venous vessels that come from the nasal sacs with the nervi olfactorii lie, some in the dorsal and some in the

ventral angle between the bulbi of opposite sides, and becoming united at the hind ends of the diverticula by dorso-ventral commissures, continue posteriorly in the hollow of the fold of the tela, and form the choroid plexus. The conditions in my 75 mm. specimen thus here so closely resemble those shown by Johnston (1911, figs. 1 and 45) both in a median view of the brain of the adult Amia and in a median sagittal section of a 25 mm. embryo of the same fish, that it is probable that the lamina supraneuroporica has a similar position in each of them, and if Johnston is correct in placing this lamina ventro-posterior to the anterior end of the bottom of the median fold of the tela in his 25 mm. Amia, it must form the anterior portion of what is actually the floor of the third ventricle of Polypterus, and not, as Bing and Burckhardt (1905) concluded, the anterior portion of the bottom of the median fold of the tela, which forms the median line of the roof of the third ventricle.

The dorsal edge of the lateral wall of the telencephalon has been everted, and there is an external sulcus extending the full length of the primordium hippocampi, approximately at the middle of the height of the lateral wall of the telencephalon, and it is particularly deep in its middle portion. The lateral edge of the tela choroidea is everywhere attached to the ventral edge of this everted portion of the lateral wall.

Nervus terminalis. What seems to be the nervus terminalis of either side is found, in my 75 mm. specimen, as two nervous strands which are wholly separate and independent of each other up to the point where they enter the nasal capsule. One of these strands arises from the dorso-lateral surface of the bulbus olfactorius, and the other from its ventral and ventro-lateral surfaces. Each strand arises by two or more rootlets which look, in sections, like protruding portions of the superficial layer of the bulbus, and each strand runs forward along the related surface of the bulbus to its anterior end. Each strand then follows the related root of the nervus olfactorius, and, as it enters the nasal capsule, fuses with its fellow. No ganglion cells could be recognised in any part of the nerve.

Nervus opticus. There is a well developed optic chiasma which lies upon the dorsal surface of the parasphenoid slightly anterior to the slight depression that lodges the hypophysis. The chiasma forms the anterior end of a marked ridge, formed by the hypothalamus, on the ventral surface of the brain, and the base of the ascending tract of the opticus is, in lateral view, separated from the chiasma by a slight furrow. From there the nervus opticus runs antero-laterally and slightly dorsally and traverses the sphenoid bone through the foramen opticum, passing, in my 75 mm. specimen, dorsal to the cartilaginous trabecula. The nerve then gradually curves somewhat more laterally and penetrates the sclerotic ventro-posterior to its central point. It is a solid nerve, without any indication of folding of any sort.

Nervus oculomotorius. This nerve, after its origin from the base of the brain, runs antero-laterally and issues from the cranial cavity through a foramen in the sphenoid common to it and the radix profundi (Allis, 1908*b*;

Lehn, 1918), the oculomotorius there lying anterior to the radix profundi. The oculomotorius then runs forward between the profundus ganglion and the cranial wall, closely pressed against the dorso-mesial surface of the ganglion, and there separates into its superior and inferior divisions. There is no slightest indication of an anastomosis with the profundus, such as Lehn found in her specimen. The superior division runs upward mesial to the ramus ophthalmicus profundus and innervates the rectus superior. The inferior division runs forward ventral to the nervus profundus and comes into intimate contact with the ciliary ganglion, there unquestionably being connected with that ganglion by strands which form the radix brevis. The nerve then continues onward, passing ventro-lateral to the rectus superior and mesial to the rectus externus and sends a branch to the rectus inferior. It then passes dorsal to the latter muscle and ventral to the nervus opticus, sends one or two branches to the rectus internus, and then passes ventral to the latter muscle and terminates in the obliquus inferior.

The course and distribution of this nerve is thus as it is in Amia excepting in that the inferior division of the nerve passes dorsal instead of ventral to the rectus inferior, this relation of the nerve to the latter muscle being, so far as I know, exceptional in the gnathostome fishes. The recti inferior and externus arise close together from the tendinous stalk that gives origin to them and also to the rectus superior, and the oculomotorius passes close to their points of origin from that stalk. A slight shifting of the point of origin of the inferior muscle would make it creep, at its origin, across the nerve, and it would then lie dorsal to it, as it does in Amia, without having either cut through the nerve or been cut through by it.

Nervus trochlearis. This nerve has the usual origin, and after a relatively long intracranial course issues from the cranial cavity through its foramen in the sphenoid. It then runs forward and becomes closely applied to the ventro-mesial surface of the ramus ophthalmicus superficialis trigemini, passes ventral to that nerve but dorsal to all the other nerves of the orbit, and enters the obliquus superior near its point of origin from the cranium.

Nervus abducens. This nerve arises, in the 75 mm. specimen, by two rootlets quite near the mid-ventral line of the brain, and from there runs antero-laterally and issues from the cranium with the nervus trigeminus through a large perforation of the cranial wall which is closed by fibrous tissue which surrounds the nerves and completely separates them from each other. That part of this tissue that encloses the abducens later undergoes chondrification, and the nerve then traverses a short canal in the cranial wall which lies postero-ventral to the foramen trigeminum and opens on the floor of the cranial cavity immediately posterior to the base of the postclinoid wall.

After issuing from its foramen the nerve runs antero-laterally ventral to the nervus trigeminus and enters and supplies the musculus rectus externus.

Nervus profundus. The root of the nervus profundus issues from the medulla, in the adult, anterior to but in contact with the root of the trigeminus,

while in the 75 mm. specimen it issues from the medulla slightly anterior to the anterior rootlet of the trigeminus. Its point of origin from the medulla indicates that its fibres are quite certainly all general cutaneous ones. The root runs forward in the cranial cavity and, in the 75 mm. specimen, traverses a perforation of the cartilaginous cranial wall that is common to it and the nervus oculomotorius and that lies anterior to the foramen trigeminum. As the two nerves traverse this perforation of the cranial wall, they are separated from each other by membrane, their two foramina, at this age, thus not being actually confluent, the primordial membranous cranial wall simply not having undergone either chondrification or ossification between the two nerves. Having issued through this foramen, a ganglion immediately forms on the root of the profundus, the nervus oculomotorius lying between this ganglion and the cranial wall and the nervus abducens lying immediately ventral to the ganglion. No communicating branch is received from the trigeminus ganglion, and no sympathetic nerve could be traced to it. There is, as already stated, no anastomosis with the nervus oculomotorius.

The radix longa arises, in the 75 mm. specimen, from the ventral surface of the profundus ganglion, and running forward enters a small ciliary ganglion which lies directly against the inferior division of the nervus oculomotorius, at the point where the branch of that nerve to the musculus rectus inferior is given off, and is there unquestionably connected with the oculomotorius by fibres that represent the radix brevis. The radix longa is not described by Lehn, but it is probably represented in that anastomosis of the profundus and oculomotorius to which she refers. From the ciliary ganglion the ramus ciliaris brevis arises, and passing between the recti superior and externus and dorsal to the rectus inferior, has a course approximately parallel to the latter muscle and perforates the sclerotic between the point of insertion of that muscle and the point where the nervus opticus enters the eyeball. Close to, or coincident with, the point where this nerve perforates the sclerotic, that cartilage is also traversed by a branch of the orbito-nasal artery and a branch of the infraorbital vein.

Anterior to the point of origin of the radix longa from the profundus ganglion, either a single branch arises from that ganglion, or two branches arise close together, the one or two branches forming the portio ophthalmici profundi shown by van Wijhe (1882) in his figure of this fish. Branches of this nerve, or nerves, run upward and forward, some passing mesial and others lateral to the ramus ophthalmicus superficialis trigemini, and, accompanying branches of the latter nerve, are distributed to tissues on the dorsal surface of the head in the region of organs 5 and 6 supraorbital. No complete anastomosis of any of these branches with the ramus ophthalmicus superficialis was noticed.

From the anterior end of the profundus ganglion the ramus ophthalmicus profundus and the ramus ciliaris longa arise, either close together or as a single trunk. The ciliaris longa runs forward between the recti superior and

externus, and passing dorsal to the nervus opticus perforates the sclerotic dorso-lateral to that nerve, between it and the point of insertion of the rectus superior, there being accompanied by a branch of the orbito-nasal artery. Lehn found this nerve arising from the ramus ophthalmicus in the transverse plane of the foramen opticum.

The ramus ophthalmicus profundus runs forward between the recti superior and externus, there lying between the superior and inferior divisions of the nervus oculomotorius, and then continues onward dorsal to the nervus opticus. A branch is here sent upward to join, but not fuse with, the ramus ophthalmicus superficialis trigemini, this branch and the main nerve both traversing a large orbital lymphatic space. Branches of this branch of the profundus perforate the roof of the orbit and are distributed to tissues on the dorsal surface of the head in the region of organ 4 supraorbital, one branch accompanying the lateralis branch to that organ. After giving off this branch the ramus ophthalmicus profundus continues onward and upward, passes ventral to the nervus trochlearis, and, in the 75 mm. specimen, ventral to the musculus obliquus superior, close to its origin in the preorbital canal. In one adult specimen that was examined the nerve also passed ventral to the obliquus superior, but in the specimen used for illustration, the nerve passes ventral to the trochlearis but dorsal to the obliquus superior. Beyond this point the nerve traverses the preorbital canal with the ophthalmicus superficialis trigemini, and on issuing from that canal lies in the antero-mesial ethmoidal groove. A branch is there sent to tissues in the region of organ 3 supraorbital, the terminal portion of the nerve then traversing the perforation in the roof of the nasal capsule at the anterior end of the ethmoidal groove and running forward in the nasal capsule accompanied by the terminal portion of the ophthalmicus superficialis trigemini and a vein and artery, as already described. As the nerve traverses the capsule one or two branches are sent upward through its roof to the region of organ 2 supraorbital, and on issuing from the capsule through the fenestra nasalis the remainder of the nerve is distributed to tissues in the region of organ 1 supraorbital, and to the extreme anterior end of the snout.

The nervus profundus of this fish thus sends branches to the entire region that, in most teleosts, is innervated by general cutaneous branches of the ramus ophthalmicus superficialis trigemini. This has been fully discussed in an earlier work (Allis, 1918*b*), and it was there said that the portio ophthalmici profundi and the ramus ophthalmicus profundus of this fish were quite certainly the homologues, respectively, of the frontal and nasal branches of the ophthalmic nerve of higher vertebrates.

Nervus trigeminus. The nervus trigeminus is currently considered to contain only general sensory and motor fibres, the communis and lateralis fibres that are associated with it being assigned to the nervus facialis. As so conceived, this nerve of the adult Polypterus arises from the medulla by a single root common to it and the nervus profundus. In the 75 mm. specimen these two

roots are wholly independent, and the nervus trigeminus arises by two rootlets, one of which is motor and the other apparently wholly general cutaneous. The root of the trigeminus, so formed, runs antero-laterally, traverses the foramen trigeminum, and then immediately swells into a large ganglion which is apparently wholly general cutaneous, the motor component of the nerve lying imbedded in the ventral surface of the ganglion. The root of the nerve, as it traverses its foramen, is accompanied by the nervus abducens, but not by any recognisable vein or artery. The ganglion lies in the trigeminus portion of the trigemino-facialis chamber, immediately anterior to that portion of the infraorbital vein that runs upward between the nervi trigeminus and facialis to fall into the ophthalmic vein, the latter vein passing dorsal to the ganglion. Dorsal to this ganglion and separated from it by the ophthalmic vein, is a ganglion formed by the fusion of two ganglia, one of which is formed on a lateralis root and the other on an intracranial branch from the communis root of the nervus facialis. The larger part of the ganglion on the lateralis root lies in the trigemino-facialis chamber, while the ganglion of the communis root is largely intracranial in position and is continuous with the intracranial portion of the facialis ganglion. The roots and ganglia of this fish thus resemble those in Scorpaena (Allis, 1909, p. 81), excepting in that the communis fibres issue from the cranial cavity with the lateralis fibres instead of with the general cutaneous ones.

From the lateralis-communis ganglion three nerves arise, the rami ophthalmicus superficialis, buccalis, and oticus, and in addition to these nerves two separate bundles of fibres are sent to the general cutaneous ganglion. The ramus ophthalmicus superficialis contains both lateralis and communis fibres, but no general cutaneous ones could be traced to it either from the general cutaneous ganglion itself, or from any of its branches. The nerve is accordingly neither an ophthalmicus facialis, an ophthalmicus lateralis, nor an ophthalmicus superficialis trigemini, as those terms are currently employed, for the two former terms are considered to designate a nerve formed exclusively of lateralis fibres, and the latter a nerve that contains a considerable proportion, at least, of general cutaneous fibres. There is also the further question as to whether the lateralis and communis fibres contained in this nerve belonged primarily to the trigeminus or to the facialis. I have accordingly thought best, as fully explained in an earlier work (Allis, 1918*b*), to readopt for this nerve the time-honoured term ramus ophthalmicus superficialis trigemini, referring, when necessary, to the lateralis or communis fibres as the lateralis or communis trigemini. Lehn calls this nerve the ramus supraorbitalis ophthalmici lateralis, and considers it to be a branch of a nerve which she calls the nervus ophthalmicus lateralis, the other branches of which are the rami infraorbitalis ophthalmici lateralis, maxillaris ophthalmici lateralis, and mandibularis externus ophthalmici lateralis. She says that an independent ramus ophthalmicus superficialis trigemini, comparable to that found in other fishes, is wanting in Polypterus.

The ramus ophthalmicus superficialis trigemini, thus defined, runs forward internal to the musculus temporalis and dorsal to all the nerves of the orbit, traverses the preorbital canal at the dorso-anterior corner of the orbit, and enters the antero-mesial ethmoidal groove on the dorsal surface of the nasal capsule. At the anterior end of that groove the nerve traverses the foramen that there perforates the roof of the nasal capsule, and runs forward in that capsule between its cartilaginous roof and the lining membrane of the nasal sac. As it traverses the orbit branches are sent upward through its roof to supply the anterior head-line of pit organs and organs 6, 5 and 4 of the supraorbital latero-sensory canal, these organs all lying on, or in, the frontal bone. As the nerve traverses the ethmoidal groove a branch is sent to organ 3 supraorbital, which lies in the nasal bone, and as it traverses the nasal capsule a branch is sent upward through the roof of the capsule to organ 2 supraorbital, which lies in the accessory nasal. The nerve then issues through the fenestra nasalis, and its lateralis component terminates in organ 1 supraorbital, which lies in the os terminale. Communis fibres doubtless accompany the lateralis fibres in all these branches of the nerve, and the branches are accompanied by general cutaneous branches of the nervus ophthalmicus profundus, as already described.

The ramus buccalis trigemini arises, like the ramus ophthalmicus superficialis, from the lateralis-communis ganglion and contains both lateralis and communis fibres. The nerve runs forward external to the musculus temporalis and then along the floor of the orbit until it reaches its anterior end. There it perforates the ventro-lateral portion of the wall of the nasal capsule, runs forward in that capsule, between its cartilaginous wall and the lining membrane of the nasal sac, passes along the dorsal surface of the ventral border of the fenestra nasalis, and, mesial to that fenestra, perforates the wall of the capsule and issues on its external surface.

Seven branches are given off by the ramus buccalis after its origin from its ganglion, this making, with the terminal branch, eight branches in all to the nerve. Two other branches, which arise directly from the lateralis-communis ganglion, belong morphologically to it, and each of these ten branches doubtless contains both lateralis and communis fibres. The terminal branch of the nerve, the one that issues from the nasal capsule antero-mesial to the fenestra nasalis, innervates organ 1 infraorbital, which lies in the median ethmoid bone. The second and third branches issue through the fenestra nasalis and innervate organs 2 and 3 infraorbital, both of which lie in the premaxillary. The fourth branch is given off just before the nerve leaves the orbit to enter the nasal capsule, and running outward innervates organ 4 infraorbital, which also lies in the premaxillary. The fifth, sixth, seventh, and eighth branches innervate the corresponding infraorbital organs, which lie, organ 5 in the lachrymal, organs 6 and 7 in the maxillary, and organ 8 in the postorbital bone. The ninth branch arises from the anterior portion of the lateralis-communis ganglion, and running upward perforates, in my 75 mm.

specimen, that overhanging portion of the dorsal end of the postorbital process of the chondrocranium that later ossifies as the sphenotic portion of the postfronto-sphenotic, and innervates organ 9 infraorbital, that organ lying in the postfrontal portion of the postfronto-sphenotic. The tenth branch of the nerve is the so-called ramus oticus facialis. It arises from the lateralis-communis ganglion, and, running upward, immediately perforates the cranial wall and enters the auditory capsule beneath the ampulla of the anterior semicircular canal. Passing ventro-lateral to that ampulla, it again enters the cartilage of the chondrocranium and issues on its dorsal surface to enter the parieto-dermopterotic bone and innervate organ 10 infraorbital, which lies in the anterior portion of the latter bone. This ramus oticus contains communis as well as lateralis fibres, but no general cutaneous ones could be traced to it, and it is not accompanied by any branch arising from the general cutaneous ganglion of the nerve.

The general cutaneous ganglion receives two bundles of communis fibres from the lateralis-communis ganglion, as above described, and still another bundle of similar fibres from a part of the facialis ganglion that lies at the base of the ramus palatinus facialis, this latter bundle forming the anastomosis described by Lehn and running upward ventro-mesial to the maxillo-mandibular vein. All of these communis fibres apparently traverse the general cutaneous ganglion and go both to the ramus mandibularis trigemini and to certain branches that have independent origin from the ganglion but belong morphologically to that nerve.

From the proximal end of the ganglion a bundle of general cutaneous fibres is sent posteriorly into the jugular canal to there join the truncus hyomandibularis facialis, and issue with it through the posterior opening of the canal. This bundle of fibres thus has a course which lies morphologically posterior to the outer wall of the jugular canal, and as that wall is probably formed (Allis, 1918*a*) by the posterior branchial-ray bar of the mandibular arch, the nerve has to the bar the relations of a facialis nerve and not of a trigeminus one. This bundle of fibres thus probably belongs to the nervus facialis, and must, accordingly, represent the primitive general cutaneous component of that nerve, a component which is otherwise wanting, and its issuing from the medulla with the general cutaneous fibres of the trigeminus, instead of as a part of the root of the facialis, is of secondary origin, and due to central condensations.

The rami maxillaris and mandibularis trigemini arise from the anterior end of the general cutaneous ganglion, and from the ganglion, close to the bases of these nerves, several small branches have their origin, these branches all containing motor fibres and hence undoubtedly belonging, morphologically, to the ramus mandibularis.

The ramus maxillaris contains only general cutaneous fibres, and runs forward through the orbit, closely accompanying the ramus buccalis throughout its entire course. Branches are sent from it to tissues of the region traversed,

and they apparently present no features of special importance. One branch enters the maxillary portion of the labial fold, toward its anterior end, and sends branches anteriorly and posteriorly in it.

The ramus mandibularis and the several smaller associated branches all contain motor, communis and general cutaneous fibres. The proximal one of the smaller branches runs antero-dorsally and in large part penetrates, on its internal surface, the muscle-mass formed by the levator arcus palatini and its derivatives, certain of the branches, however, passing outward across the anterior edge of the levator and then posteriorly a short distance along its external surface. The next one or two branches arise in the angle between the rami maxillaris and mandibularis and are sent the one to the musculus temporalis and the other to the pterygoideus, the branch to the temporalis penetrating it on its internal surface and that to the pterygoideus penetrating it on its dorso-external surface. The next two branches arise from the base of the ramus mandibularis and not directly from the ganglion, and are the one largely motor and the other wholly sensory. The motor branch goes to the large superficial portion of the adductor mandibulae, entering it on its internal surface. The sensory branch runs outward across the anterior edge of the superficial portion of the adductor and then postero-ventrally along its external surface, some of its branches penetrating the muscle, this branch thus apparently corresponding to the ramus posttrematicus externus anticus of the more posterior arches.

After giving off these several branches, which doubtless vary somewhat in different specimens, the ramus mandibularis runs downward along the dorso-external surface of the musculus pterygoideus, and while in that position sends a branch to the deeper portion of the adductor, the branch entering the muscle on its external surface. The nerve then passes internal to the deeper portion of the adductor, crosses the internal surface of that muscle, and then turns forward, there either passing over the hind edge of the muscle, onto its external surface, or traversing the muscle near its hind edge and close to its origin (figs. 42–44). The nerve then enters the ramus of the mandible, there lying, in my 75 mm. specimen, internal to those fibres of the superficial portion of the adductor that pass directly into the ramus of the mandible, but external to the tendon of insertion of the musculi temporalis and pterygoideus, and also external to those fibres of the mandibular portion of the adductor that have their insertions on the latter tendon. Luther (1913, p. 21) shows this nerve passing internal to this tendon and muscle, but it was not so found in any of my specimens. No motor fibres going to the mandibular portion of the adductor could be traced in the sections of my 75 mm. specimen, but the nerve, in this part of its course, sends a small sensory branch outward to join the ramus mandibularis internus facialis as that nerve traverses its canal in the dermarticular.

As the ramus mandibularis here passes between the two parts of the adductor, it gives off a branch which is wholly sensory and soon separates into

two parts. One of these parts runs forward dorsal to that ridge on the internal surface of the dentary that forms the dorsal edge of the groove that lodges Meckel's cartilage and gives support to the dorsal edge of the splenial, and is there joined by the ramus mandibularis internus facialis, not shown in the figures, the two nerves lying in the groove between the dentigerous edges of the dentary and splenial. The other part of the branch runs forward ventral to the ridge, above referred to, on the mesial surface of the dentary, there lying along the dorsal surface of Meckel's cartilage and soon entering a canal in the dentary which begins at about the anterior quarter of the entire length of the mandible. A branch is there at once sent outward through the bone, and entering the mandibular portion of the labial fold turns posteriorly in it. The remainder of the nerve then continues onward in the canal in the dentary, accompanied by an arterial vessel, and sends branches to the dentary teeth. Both portions of this branch of the ramus mandibularis thus have a course dorsal to Meckel's cartilage, that is, morphologically along its internal surface. The branch is accordingly the ramus posttrematicus internus trigemini and corresponds strictly in its relations to the dentary and to Meckel's cartilage to the inferior dental nerve of human anatomy (Bryce, 1915, fig. 92).

After giving off this branch, the remainder of the ramus mandibularis runs antero-ventrally across the external (morphologically anterior) surface of Meckel's cartilage, in the groove on the internal surface of the dermarticular that was described when describing that bone, and is there joined by the ramus mandibularis externus facialis, the two nerves then running forward ventral (morphologically external) to Meckel's cartilage, in a groove on the mesial surfaces of the dermarticular and dentary, and being accompanied by a branch of the mandibular artery. The two nerves here pass ventral to the musculus geniohyoideus inferior, close to its line of origin, but are not seen in ventral views because of the underhanging ventral edge of the mandible. As the ramus mandibularis passes over the hind edge of the geniohyoideus inferior it gives off either a single branch which immediately separates into two branches, or two branches arising close together. These two branches contain some sensory fibres and all the remaining motor fibres of the nerve, and they run antero-mesially along the ventral surface of the geniohyoideus inferior, and then turn, the one anteriorly and the other posteriorly, each of them sending branches into the muscle to innervate it. The anterior branch does not continue beyond the muscle. The posterior branch continues posteriorly beyond it and reaches the ventral surface of the geniohyoideus superior, where it breaks up into branches which penetrate that muscle and innervate it. The terminal branch of the nerve usually, but not always, runs directly into a branch of the ramus hyoideus facialis, the two nerves there forming a continuous circuit, as the corresponding nerves do in Amia and Scomber. This has been fully discussed in a recent work (Allis, 1919*d*), and it was there shown that the fibres of the ramus mandibularis trigemini are all sent to the geniohyoideus, and that the musculus hyohyoideus is innervated wholly by the

nervus facialis. After giving off this important branch to the two divisions of the geniohyoideus, the ramus mandibularis continues onward in the groove on the mesial surface of the dentary, sending branches outward with each of the branches of the mandibularis externus facialis to the latero-sensory organs of the mandibular canal, the branches of the trigeminus innervating the general sensory tissues of the region.

This terminal portion of the ramus mandibularis thus corresponds, in its relations to Meckel's cartilage and its terminal distribution, to the nervus mylohyoideus of human anatomy (Bryce, 1915, fig. 92), but there is no branch that corresponds to the nervus lingualis unless it be that part of the ramus posttrematicus internus that runs forward in the groove between the dorsal (oral) edges of the dentary and splenial; and the fact that that part of the nerve is accompanied by the mandibularis internus facialis seems to indicate that it is the lingualis.

Nervus facialis. The nervus facialis arises, in the adult, by a single root which issues from the medulla slightly posterior to the root of the trigeminus and in contact, posteriorly, with the root of the nervus acusticus. In the 75 mm. specimen it arises by four rootlets, two lateralis, one communis, and one motor, the two lateralis rootlets furnishing, the one the lateralis fibres to the nervus trigeminus and the other those to the nervus facialis. The communis root soon becomes ganglionated, and then separates into two parts, one destined to the nervus trigeminus and the other to the nervus facialis. Those parts of the lateralis and communis roots that are destined to the nervus trigeminus run forward in the cranial cavity, and, joining the root of the latter nerve, issue with it through the trigeminus foramen. These two bundles of fibres thus here definitely belong, both in their point of exit from the cranial cavity and in their peripheral distribution, to the nervus trigeminus, and, as already stated, I consider them to belong to that nerve and not to the nervus facialis.

After giving off these two bundles of fibres to the nervus trigeminus, the remainder of the facialis root, composed of lateralis, communis and motor fibres, traverses the primary facialis foramen and enters the jugular canal in the lateral wall of the cranium, there lying ventral to the vena jugularis. Ganglion cells then immediately appear in the lateralis component of the root, and the communis component, which is still ganglionated, separates into two parts, one of which extends forward in the jugular canal and the other posteriorly in it. The anterior portion of this communis ganglion gives origin to the ramus palatinus, and to the bundle of communis fibres, already referred to, that is sent to the general cutaneous ganglion of the nervus trigeminus, and it is connected, by an extracranial communicating branch, with the communis ganglion of the nervus glossopharyngeus. The fibres that arise from the posterior portion of the ganglion join the lateralis and motor fibres of the nervus, and together form the truncus hyomandibularis, this truncus receiving the communicating branch from the general cutaneous ganglion

of the trigeminus, already described. Sympathetic fibres are sent from the main sympathetic chain both to that portion of the communis ganglion that is related to the truncus hyomandibularis and to the part related to the ramus palatinus.

The ramus palatinus, or more properly ramus anterior facialis, issues through the anterior opening of the jugular canal and enters the trigeminus chamber, where it turns sharply downward onto the dorsal surface of the horizontal plate of the ascending process of the parasphenoid, passing dorso-lateral to the ophthalmic branch of the common carotid artery, close to its point of separation from the latter artery. The nerve, still containing ganglion cells, then runs forward dorso-lateral to the common carotid artery, and after receiving the communicating branch from the nervus glossopharyngeus, gives off the communicating branch to the general cutaneous ganglion of the nervus trigeminus. The latter branch runs upward, dorso-lateral to the infra-orbital branch of the vena jugularis, and as its fibres apparently all go to the ramus mandibularis trigemini, as already stated, it is the ramus pretrematicus externus of the facialis. The ramus palatinus, still ganglionated, here becomes slightly enlarged, thus forming a slight ganglion at the base of the nerve, and ganglion cells are not continued forward beyond this point. From the anterior end of this small ganglion, or from the base of the ramus palatinus immediately anterior to it, a branch is given off which runs forward a short distance parallel to the palatinus, in the dense connective tissues that bind the palato-quadrate to the ventral surface of the lateral edge of the parasphenoid, there lying dorso-lateral to the dorso-mesial edge of the entopterygoid. It then separates into two branches both of which run ventrally between the entopterygoid and the palatoquadrate cartilage and are distributed to the ventro-mesial surface of the latter cartilage. This branch must therefore be a ramus pretrematicus internus facialis, as that nerve is defined by Sewertzoff (1911), but if it contains fibres derived from the communicating branch from the nervus glossopharyngeus, it would be, in part, also a ramus pharyngeus glossopharyngei corresponding to that nerve as described by me in Amia (Allis, 1897, p. 685).

The ramus palatinus then continues onward along the dorsal surface of the lateral edge of the parasphenoid, lateral to the common carotid artery and ventral to the musculus pterygoideus, until it reaches the anterior edge of the latter muscle. There it passes downward over the lateral edge of the parasphenoid, and runs forward, at first immediately dorsal to the connective tissue that binds the palatoquadrate to the parasphenoid, and then enclosed within that tissue, there lying considerably dorso-mesial to the dorso-mesial edge of the palatoquadrate cartilage. The nerve then gives off a branch which runs antero-latero-ventrally along the internal surface of the palatoquadrate cartilage, between it and the entopterygoid and ectopterygoid, and, beyond the lateral edge of the palatoquadrate cartilage, enters a canal in the entopterygoid and issues from that bone near its lateral edge. There it continues forward

and can be traced a certain distance, communicating branches connecting it with the ramus maxillaris trigemini. This branch of the palatinus thus corresponds to the ramus palatinus posterior of Amia, and as it lies internal to the palatoquadrate cartilage it would seem as if it must be a ramus pretrematicus internus facialis, there thus being two of these nerves in this fish, one anterior and the other posterior.

After giving off this branch, the remainder of the nerve becomes the ramus palatinus anterior, or ramus pharyngeus facialis, and runs forward, in the tissues dorsal to the entopterygoid, to the anterior end of that bone. It then passes beneath the nasal capsule, there lying at first in the tissues immediately mesial to the mesial dermopalatine (the so-called vomer), and then dorsal to the latter bone. It is accompanied, throughout this part of its course, by a small vein and artery.

The truncus hyomandibularis facialis runs posteriorly in the jugular canal and issues through its posterior opening, being joined, while in the canal, by the communicating branch of general cutaneous fibres from the trigeminus ganglion. The truncus then runs outward ventral to the vena jugularis, and soon separates into its rami mandibularis and hyoideus, the ramus opercularis being a branch of the latter nerve.

The ramus mandibularis contains all of the lateralis fibres of the nerve, some of the communis fibres, and, so far as could be judged from my sections, a considerable portion of the general cutaneous fibres received from the trigeminus ganglion, but no motor fibres. The nerve runs postero-ventrally along the mesial wall of the spiracular canal, there lying at first dorsal and then lateral to the efferent artery of the hyal arch, the nerve and artery both lying in a fold of the mucous tissues that projects ventrally between the posterior portion of the spiracular canal, externally, and the dorso-anterior end of the first gill cleft internally. At the hind edge of the spiracular canal the nerve turns ventro-laterally across that edge, between it and the anterior edge of the hyomandibula and then downward along the lateral surface of the canal, there lying along the line of insertion of the musculus protractor hyomandibularis, and internal to the superficial division of the adductor mandibulae, between the latter muscle and the external wall of the dorso-anterior diverticulum of the first gill cleft. There the nerve gives off its first branch, which runs ventro-posteriorly and supplies both the dorsal one of the three laterosensory organs in the preoperculum, and the organs of the posterior horizontal and vertical cheek-lines of pit organs. Fibres that are not lateralis ones certainly form part of this branch and go to tissues of the region, but whether they are communis or general cutaneous ones could not be definitely determined, and the same is true for the other branches of the nerve. A second and similar branch is then sent to the seventh preoperculo-mandibular organ, and approximately at the point of origin of this branch the ramus mandibularis separates into its external and internal branches.

The ramus mandibularis externus contains all of the lateralis fibres of the

ramus mandibularis and also some of the other fibres of that nerve and is apparently the ramus posttrematicus externus anticus facialis (Allis, 1920*b*). It runs downward internal to that part of the superficial division of the adductor mandibulae that has its origin on the hyomandibula, but external to the tough membrane that here covers the latter bone, and then passes internal to that slip of the tough membrane that covers the external surface of the palatoquadrate that has its insertion on the hyomandibula. Ventral to that slip it sends a branch to the sixth preoperculo-mandibular organ, the nonlateralis fibres related to this branch sometimes appearing as a separate and independent branch. The main nerve then turns ventro-anteriorly along the hind edge of the palatoquadrate, and passing external to the quadrato-hyomandibular articulation, and posterior and external to the quadrato-mandibular articulation, reaches the hind end of the mandible, where it enters the canal that lies, at first, between the dermarticular and autarticular, but farther forward entirely in the former bone. While in that canal two branches are sent outward, one going to the fifth and the other to the fourth preoperculo-mandibular organs, these two organs both lying in the dermarticular. The nerve then issues from the canal in the dermarticular and enters that groove on the mesial surface of the dentary that first passes external to Meckel's cartilage and then forward along the ventral edge of that cartilage and lodges also the ramus mandibularis trigemini. There branches are sent to the third and second organs of the preoperculo-mandibular canal, the terminal branch of the nerve going to the first organ of that canal.

The ramus mandibularis internus, which is the posttrematicus internus facialis, turns antero-ventrally after its separation from the ramus externus and either passes through a notch, or a foramen, at the dorso-posterior corner of the metapterygoid. It then continues onward along the hind edge of the palatoquadrate, passing internal to the quadrato-hyomandibular articulation and postero-ventral to the quadrato-mandibular articulation, and reaches the mandible. There it enters the short canal that begins on the mesial surface of the autarticular, directly ventral to the mesial end of the articular facet for the quadrate, and issues from that canal onto the mesial surface of the hind end of Meckel's cartilage. There it runs antero-dorsally across Meckel's cartilage and enters the groove between the splenial and the dentigerous edge of the dentary, where it runs forward to the anterior end of the mandible, accompanying that branch of the ramus mandibularis internus trigemini that also occupies that groove. This nerve of Polypterus thus has to Meckel's cartilage the relations of the chorda tympani of human anatomy (Bryce, 1915, fig. 92), which is further evidence that it is the homologue of that nerve.

The ramus hyoideus facialis runs posteriorly internal to the hyomandibula, and immediately gives off its ramus opercularis, which contains both sensory and motor fibres, the former apparently being communis ones. This ramus runs posteriorly mesial to the hyomandibula and dorsal to the opercular process of that bone, receives a communicating branch from the ramus anterior

glossopharyngei, and then reaches the external surfaces of the musculi adductor hyomandibularis and adductor operculi, where it runs posteriorly, sending branches to both those muscles and to tissues of the region. A terminal branch of the nerve runs directly into a terminal branch of the supratemporal branch of the nervus vagus, the two nerves forming a continuous circuit which is topographically similar to that in Amia (Allis, 1897), but different from that in Menidia (Herrick, 1899). Lehn found this nerve lying ventral to the opercular process of the hyomandibula.

After giving off the ramus opercularis, the ramus hyoideus turns outward across the dorsal edge of the opercular process of the hyomandibula, there passing between the hind edge of the latter bone and the stout ligament that extends from the opercular process upward to the accessory hyomandibula. The nerve then runs ventrally in the gill cover, lying slightly posterior to the hyomandibula and epihyal and sending branches posteriorly and postero-ventrally internal to the opercular bones, these branches innervating the musculus hyohyoideus superior and tissues of the region. At the level of the proximal (posterior) end of the ceratohyal the nerve passes onto the external surface of the hyohyoideus inferior, and is distributed to that muscle and adjacent tissues. One branch of the nerve passes onto the external surface of the geniohyoideus superior and usually there anastomoses with that terminal branch of the trigeminus that innervates the latter muscle, another branch passing internal to the geniohyoideus superior and anastomising with a branch of the ramus posttrematicus glossopharyngei.

Nervus acusticus. This nerve arises by a large root which lies immediately posterior to, and in contact with, the lateralis root of the nervus facialis. In the adult this root may issue from the medulla as two separate roots, a ramus anterior (vestibularis) and a ramus posterior (cochlearis). The ramus anterior, when found as a separate root, separates into two parts, one of which supplies the maculae of the ampulla anterior, ampulla externa, and recessus utriculi, and the other the maculae sacculi and neglecta. The ramus posterior supplies first the macula lagenae and then the macula of the ampulla posterior. I thus find this nerve as described by Retzius (1881), excepting in that the ramuli said by him to go to the maculae sacculi and neglecta form part of the anterior, instead of the posterior ramus of the nerve.

Nervus glossopharyngeus. This nerve arises, in the adult, as well as in the 75 mm. specimen, by two rootlets which lie close together, ventral and slightly posterior to the root of the nervus lineae lateralis vagi. One of the rootlets contains the motor, and the other the sensory fibres of the nerve, the latter fibres apparently all being communis ones. This root soon receives a bundle of lateralis fibres from the root of the nervus lineae lateralis vagi, and, running postero-laterally, enters and traverses the recessus sacculi, there passing ventral to all parts of the membranous ear and to all branches of the nervus acusticus. The nerve then issues from the cranium through the glossopharyngeus foramen, there lying ventral to the vena jugularis and being

accompanied, as it traverses its foramen, by a delicate branch of that vein, a similar but much larger branch issuing with the nervus vagus through its foramen.

Immediately after issuing from its foramen the nervus glossopharyngeus gives off, in the 75 mm. specimen, a branch which contains both communis and lateralis fibres, and an independent ganglion, involving both components, immediately forms upon it. From this ganglion a ramus supratemporalis arises, this nerve containing all the lateralis fibres of the glossopharyngeus and a part of the communis fibres. It runs dorsally along the lateral surface of the cranium, passes mesial to the vena jugularis, and then traverses a canal in the opisthotic and issues on the dorsal surface of that bone. There it separates into two branches, one of which penetrates the parieto-dermopterotic and innervates organ 11 of the main infraorbital canal, the other anastomosing with two branches of the ramus supratemporalis vagi and going to the organs of the middle head-line of pit organs. The latter branch of the glossopharyngeus apparently contains only communis fibres, while the vagus branches apparently contain lateralis fibres, and if this be correct the middle head-line of pit organs would be innervated by the vagus.

After giving off this branch, the nervus glossopharyngeus receives a communicating branch from the first vagus ganglion and then runs dorso-laterally across the postero-mesial edge of the epibranchial of the first branchial arch, and reaches the dorsal surface of that element. There it swells into an elongated ganglion which lies along the lateral surface of the cranium, ventral to the vena jugularis. From the hind end of this ganglion the ramus posttrematicus glossopharyngei arises, and from its anterior end the ramus anterior glossopharyngei.

The ramus anterior lies, in the 75 mm. specimen, along the dorsal surface of the thymus, but gives off a small branch which traverses that gland and rejoins the main nerve at its anterior end. The ramus anterior there gives off a branch which runs posteriorly between the two heads of the levator muscle of the first branchial arch and then along the external surface of that muscle, and reaches the external surface of the ceratobranchial of its arch, where it runs downward in the arch, always lying anterior to the ramus posttrematicus glossopharyngei. This branch of the ramus anterior is accordingly the ramus posttrematicus externus anticus. As it passes over the hind edge of the levator of the arch, it crosses, externally, a ramus posttrematicus internus, to be later described, and may there anastomose with that nerve, these nerves and the ramus anterior then forming a loop around the levator. After giving off this branch, the ramus anterior gives off, in the 75 mm. specimen, two branches, both of which run postero-ventrally, one lying along the ventral surface of the musculus adductor hyomandibularis and dorsal to the efferent artery of the hyal arch, and the other ventral to that artery, close to the ramus mandibularis facialis. The dorsal one of these two branches is connected, by an anastomosing branch, with the ramus opercularis facialis, the anastomosing

branch passing across the anterior edge of the adductor hyomandibularis. These two branches of the nerve both lie immediately lateral (internal) to the mucous lining membrane of the lateral wall of the dorsal, pocket-like end of the first branchial cleft, and hence are both pretrematic nerves, the ventral one being a pretrematicus internus and the other apparently a pretrematicus externus. The remainder of the ramus anterior, which is now the ramus pharyngeus glossopharyngei, runs forward through the canalis parabasalis in the ascending process of the parasphenoid—there lying ventral to the efferent artery of the hyal arch and lateral to the common carotid artery—and fuses with the small ganglion at the base of the ramus palatinus facialis, slightly proximal to the point of origin of the communicating branch from that ganglion to the general cutaneous ganglion of the nervus trigeminus. This branch of the glossopharyngeus is described by Lehn as the ramus palatinus, and it would seem to represent Jacobson's nerve, but it fuses entirely with the palatinus portion of the geniculate ganglion, instead of receiving a branch from that ganglion and then continuing onward to end in an otic ganglion. Furthermore, the nerve apparently contains only communis fibres, and Norris says (1908, p. 547) that Jacobson's nerve is largely composed, in the Amphibia, of general cutaneous fibres, with but few communis and sympathetic ones.

The ramus posttrematicus, immediately after its origin from the hind end of the glossopharyngeus ganglion, sends a motor branch to the levator muscle of the first branchial arch, and then runs outward posterior to that levator. It then immediately gives off a sensory branch which passes internal to the ramus posttrematicus externus anticus, and may, as already stated, anastomose with that nerve. This branch then perforates, from its external surface and near its dorsal edge, the stout ligament that extends from the latero-ventro-posterior corner of the ascending process of the parasphenoid to the dorsal end of the first ceratobranchial, and reaches the internal edge of the latter ceratobranchial, where it runs downward in its arch, lying close to, or fusing with, the ramus pretrematicus internus of the first vagus nerve. This branch of the glossopharyngeus is thus a ramus posttrematicus internus. Soon after giving off this sensory branch, the ramus posttrematicus crosses the external surface of the epibranchial of the first branchial arch, there lying in the groove between that element of the arch and the pharyngobranchial, and reaches the external surface of the ceratobranchial, where it lies between the bases of the two rows of cartilaginous branchial rays. There it is joined by the ramus pretrematicus externus of the first vagus nerve, this branch apparently being a general cutaneous one and fusing completely with the ramus posttrematicus glossopharyngei. The trunk so formed continues downward in the arch, and soon sends a branch to the tissues of the arch, this branch apparently containing motor fibres destined to innervate certain small muscles related to the gill filaments. Near the ventral end of the arch two branches are sent to the musculus interarcualis ventralis of the arch, and between these two branches the ramus posttrematicus forms an anastomosis with a branch of

the ramus hyoideus facialis, as already described. Beyond this point the nerve anastomoses completely with the terminal portion of the ramus pretrematicus internus of the first vagus, the nerve so formed continuing onward along the internal surface of the tissues that form the floor of the buccal cavity.

Nervus lineae lateralis vagi. This nerve arises from the medulla slightly dorsal and anterior to the root of the glossopharyngeus, and immediately sends a branch to the latter root. The root then becomes imbedded in the lateral surface of the large intracranial vagus ganglion and issues from the cranial cavity through the vagus foramen with the vagus nerve and a large venous vessel which joins the vena jugularis. As the root issues through the vagus foramen it separates into two parts and a ganglion forms on each of them, one being the ganglion of the ramus supratemporalis and the other that of the nervus lineae lateralis. The latter nerve was not further traced. The ramus supratemporalis passes ventro-anterior to the venous vessel that issues through the vagus foramen, and then runs dorso-laterally mesial to the posterior process of the opisthotic, in the hollow between that process and the body of the bone. Branches are sent by it to organs 12 and 13 of the main infraorbital latero-sensory canal, which lie the one in the first supratemporal bone and the other in the posttemporal (suprascapular), then two separate branches to the middle head-line of pit organs, and the nerve then terminates in branches to the two supratemporal organs, which lie in the second and third supratemporal bones.

Nervus vagus. The nervus vagus arises by several rootlets which contain motor, communis and general cutaneous fibres. A large intracranial ganglion forms on the general cutaneous fibres and protrudes partly through the vagus foramen, and two extracranial ganglia are formed on the communis fibres of the nerve, one in relation to the fibres destined to the first vagus nerve and the other on the remaining fibres of the nervus.

The ramus supratemporalis vagi of the 75 mm. specimen arises by two roots from the dorsal surface of the protruding, extracranial portion of the general cutaneous ganglion, each root receiving a bundle of communis fibres. One root runs upward dorso-posterior, and the other ventro-anterior to the vein that issues through the vagus foramen, the two then fusing with each other and joining the ramus supratemporalis of the nervus lineae lateralis. The nerve is in part distributed to tissues on the dorsal surface of the head, but two important branches run laterally over the dorsal edge of the musculus adductor operculi, and then ventrally along the external surface of that muscle. One of these branches fuses with the ramus opercularis facialis, the other passing external to that nerve and being distributed to tissues in the gill cover, this distribution of this branch of the vagus evidently showing that that cover was not developed wholly in relation to the hyal arch.

The first vagus nerve arises, with the other vagus nerves, from the ventral portion of the intracranial ganglion, and separates from the other vagus nerves while they are all traversing the vagus foramen, the first vagus there lying ventral to the other nerves, and all of them lying ventral to the distal

end of the general cutaneous ganglion of the complex. The nerve consists mainly of motor and communis fibres, but some general cutaneous fibres must certainly enter it, for, as there are certainly general cutaneous tissues in the arch the nerve traverses, there must be nerve fibres to innervate them. Furthermore, although no general cutaneous fibres could be definitely traced into this nerve, they were traced into the nerves sent to the more posterior arches. After the nerve has separated from the other nerves of the complex, a small and independent ganglion is formed in relation to its communis fibres, this ganglion forming, as in Amia (Allis, 1897, fig. 59), a knob-like swelling on the anterior surface of the main trunk of the nerve. From this ganglion, in the 75 mm. specimen, four nerves arise, and the descriptions that follow, of this nerve and the other vagus nerve, apply largely to this specimen.

One of the nerves that arise from the first vagus ganglion is a communicating branch to the nervus glossopharyngeus, and it has already been referred to when describing that nerve.

A second nerve separates into two parts. One of these parts immediately joins and fuses with the main sympathetic nerve, but the nerve so formed soon separates into two parts, one of which is certainly largely composed of sympathetic fibres and the other largely of communis fibres. Both of these nerves run forward and traverse the canalis parabasalis in the ascending process of the parasphenoid, the sympathetic nerve then falling into the trigeminus ganglion and the communis one joining and closely accompanying the ramus palatinus facialis proximal to the point where the communicating branch is sent from that nerve to the trigeminus ganglion, this nerve thus being the ramus pharyngeus of the first vagus nerve. The other part of this second nerve of the first vagus perforates the thymus, and while in that gland receives a communicating branch from the communis nerve just above described. The nerve so formed then enters the first branchial arch and reaches the internal surface of that arch, where it joins and fuses with the ramus posttrematicus internus glossopharyngei. This branch of the first vagus is thus the ramus pretrematicus internus of that nerve, and the nerve formed by its fusion with the ramus posttrematicus internus glossopharyngei is the ramus internus of the first branchial arch. This nerve runs downward along the internal surface of the arch, and, at its ventral end, joins and fuses with the terminal portion of the ramus posttrematicus glossopharyngei, as already described.

The third nerve that arises from the first vagus ganglion runs outward between the levator muscles of the first and second branchial arches, and separates into two parts. One of these parts is the ramus pretrematicus externus of the first vagus, and joins the ramus posttrematicus glossopharyngei on the external surface of the first arch. The other part is the ramus posttrematicus externus anticus of the first vagus, and it has a course, in its arch, similar to that of the corresponding branch in the glossopharyngeus arch.

The remaining branch that arises from the first vagus ganglion is the ramus posttrematicus. This nerve first sends a motor branch to the levator muscle

of its arch, and then both in my 75 mm. specimen and in one adult that was examined, runs outward through that muscle. On issuing from the muscle it gives off its ramus posttrematicus internus, which immediately joins and fuses with the ramus pretrematicus internus of the second vagus. The main nerve then receives, and fuses with, the ramus pretrematicus externus of the second vagus, and, running downward in its arch, gives off first a branch which contains motor fibres, apparently destined to muscle fibres related to the gill filaments, then a branch which is apparently wholly sensory, and then a third branch which innervates the musculus interarcualis ventralis of its arch. The remainder of the nerve then separates into two branches, each of which anastomoses with the ramus internus of the arch.

The second vagus nerve arises from the main extracranial ganglion of the vagus complex, and contains motor, communis, and a few general cutaneous fibres. It immediately gives off a motor branch to the levator muscle of its arch, and a communis branch which goes to the dorsal surface of the branchial chamber in the region of the basioccipital, and then runs outward anterior to the levator muscle of its arch. The nerve then gives off, in succession, a ramus pretrematicus internus, a ramus pretrematicus externus, a ramus posttrematicus externus anticus, and a ramus posttrematicus internus; all of these nerves having courses similar to those of the corresponding nerves in the preceding arches. The remainder of the nerve is then the definitive ramus posttrematicus, which runs downward in its arch, gives off branches similar to those of the first vagus, and then separates into two parts, each of which fuses with one of two terminal branches of the ramus internus of the arch.

The third vagus nerve arises from the extracranial ganglion of the complex and soon sends a motor branch to the levator muscle of its arch. It then runs outward anterior to that levator and gives off, in succession, a ramus pretrematicus internus, a ramus pretrematicus externus, a ramus posttrematicus externus anticus, and a ramus posttrematicus internus, these nerves all having courses similar to those in the preceding arches, excepting in that the ramus posttrematicus externus anticus fuses completely with the ramus posttrematicus throughout the larger part of its course. The ramus posttrematicus runs downward in its arch giving off branches similar to those in the preceding arches, and finally anastomosing with the ramus posttrematicus internus of its own arch, exactly as, in the more anterior arches, it anastomoses with that nerve fused with the ramus posttrematicus internus of the next posterior arch. No pharyngeal branch was found related to this nerve.

The remaining vagus nerve, the ramus intestinalis, was not traced beyond its origin from the extracranial ganglion of the complex, but branches of the nerve innervate the superior and inferior pharyngo-claviculares, and the transversus ventralis.

SUMMARY

The cranium of Polypterus is platybasic, and several of the cranial bones correspond, in topographical position and relations, to two or more of the bones of recent Holostei and Teleostei. These several bones are the basi-exoccipital (basioccipital + exoccipitals), the parieto-dermopterotic (parietal + dermopterotic), the postfronto-sphenotic (autosphenotic + dermosphenotic), the premaxillary (premaxillary + antorbital + ½ dermoethmoid), the maxillary (maxillary + suborbitals), the cheek-plate (preoperculum + cheek-plate), and the sphenoid (orbitosphenoids + alisphenoids + piscine basisphenoid + proötic bridge). The nasal, accessory nasal and os terminale, found wholly separate in this fish, are usually represented by a single bone in other fishes. There is a large opisthotic, which is partly of primary and partly of secondary origin and invades somewhat the regions occupied, in other fishes, by the epiotic, autopterotic and proötic, the two former bones, as independent ossifications, being wholly wanting in this fish, and the proötic either also wanting, being found as a small and unimportant bone, or, possibly, found fused with the ascending process of the parasphenoid.

The opisthotic, so well developed in this fish, is found as a dermal, and often unimportant, bone in the Holostei and most of the Teleostei; the epiotic, absent in Polypterus, is found in both the Holostei and Teleostei; and the autopterotic, also absent in Polypterus, is found in the Teleostei but not in the Holostei. In the Teleostei there are thus five otic bones, the sphenotic, pterotic, epiotic, proötic and opisthotic, but the opisthotic is tending to disappear, this apparently being correlated to the development of the autopterotic. In the Tetrapoda, a proötic, alone, is found in the Batrachia (Gaupp, 1905), a proötic and opisthotic in Reptilia, a proötic, opisthotic and epiotic in Aves, and several otic bones in the Mammalia, Huxley giving three, but Vrolik six. A sphenotic, found in Polypterus and in the Holostei and Teleostei, is not described as such in any of the Tetrapoda, but one of the centres of ossification ascribed to the proötic in man has markedly the position of the piscine autosphenotic, for it is said to appear on the dorso-lateral aspect of the otic capsule, over the superior (anterior) semicircular canal, to form the "border" over the nervus facialis, and to extend into the tegmen tympani from above, all of which would be characteristics of an enlarged autosphenotic and not of the piscine proötic.

The dental arcade is apparently similar to that in the Mammalia, and, in fishes, this arcade is known only in the Crossopterygii. The superior maxillary bone has certain striking resemblances to that of the Mammalia.

The trigemino-facialis chamber consists of a trigeminus chamber and a jugular canal, the latter canal apparently representing a primitive condition of the facialis part of the entire chamber. The lateral wall of the trigeminus chamber is formed by the ascending process of the parasphenoid, instead of, as in the Holostei and Teleostei, by the proötic.

The hyomandibula corresponds to the prefacialis portion of the holostean and teleostean hyomandibula, the postfacialis portion of the latter element being represented by ligament.

The common carotid artery traverses the canalis parabasalis through the ascending process of the parasphenoid and enters the ventral portion of the trigeminus chamber, where it gives off an ophthalmic branch, which accompanies the ramus ophthalmicus superficialis trigemini. The remainder of the artery issues into the orbit and there runs forward along the lateral edge of the parasphenoid, in the position of the orbito-nasal artery of the Teleostei, but the artery still contains the equivalents of the internal carotid, of a part of the external carotid, and of the orbito-nasal artery of the latter fishes. As this artery approaches the foramen opticum it gives off first a maxillo-mandibularis branch, and then two branches which enter the cranial cavity posterior to the nervus opticus and are, the one the arteria cerebralis posterior and the other the arteria cerebralis anterior. The remainder of the artery is then the orbito-nasal artery. The internal carotid of this fish thus enters the cranial cavity by passing dorsal, instead of ventral, to the trabecula, a condition which is also found in Amiurus (and hence probably in others of the Siluridae) but in no other fish that I know of.

The jugular vein is formed by the union of supraorbital and infraorbital veins, the supraorbital one accompanying the ramus ophthalmicus superficialis trigemini, and receiving, at its base, the maxillo-mandibularis vein, while the infraorbital one accompanies the common carotid and orbito-nasal arteries.

The nervus terminalis is apparently represented by two nervous strands that arise from the bulbus olfactorius and accompany the nervus olfactorius into the nasal sac.

The eye-muscles are innervated as they are in the Ganoidei and Siluridae, excepting in that the inferior division of the nervus oculomotorius passes dorsal, instead of ventral, to the musculus rectus inferior.

The radix profundus, which apparently contains only general sensory fibres, issues from the cranial cavity with the nervus oculomotorius, and a ganglion then immediately forms upon it. No branches from other nerves could be traced to this ganglion, and from it three nerves arise: the radix longa, which runs forward with the nervus oculomotorius and enters the ciliary ganglion, which is sessile on the inferior division of the nervus oculomotorius; a ramus ophthalmicus profundus, which runs forward between the two divisions of the oculomotorius and then ventral to the nervus trochlearis and joins, but does not fuse with, the ramus ophthalmicus superficialis trigemini as it traverses the preorbital foramen; and a portio ophthalmici profundi, which runs forward in the orbit, but not beyond it, lying ventral to the ramus ophthalmicus superficialis trigemini and sending branches to the dorsal surface of the head, accompanying branches of the latter nerve. The profundus nerve of this fish thus sends branches to the entire region that, in most teleosts, is innervated by branches of the ramus ophthalmicus superficialis trigemini,

its ramus ophthalmicus corresponding to the ophthalmic nerve of man and its portio ophthalmici to the frontal branch of that nerve.

The nervus trigeminus contains motor, general sensory, communis, and lateralis fibres, the communis and lateralis fibres arising from the medulla with the corresponding roots of the nervus facialis. These fibres all issue from the cranial cavity through the foramen trigeminum and enter the trigeminus chamber, where two separate ganglia form, one on the general sensory fibres and the other on the lateralis-communis ones. From the lateralis-communis ganglion the rami oticus, ophthalmicus superficialis and buccalis arise, all of which contain both lateralis and communis fibres, and important bundles of communis fibres are also sent to the general sensory ganglion. The latter ganglion also receives communis fibres from the ramus palatinus facialis, and it sends a bundle of general sensory fibres into the jugular canal to there join and fuse with the truncus hyomandibularis facialis. From the general sensory ganglion the rami maxillaris and mandibularis arise, the former apparently containing only general sensory fibres, and the latter motor, general sensory and communis ones.

The radix facialis apparently contains only motor, lateralis, and communis fibres, but it receives the bundle of general sensory fibres just above mentioned from the nervus trigeminus. The radix issues from the cranial cavity into the jugular canal, and a ganglion forms on it which is partly intracranial and partly extracranial in position. From this ganglion the rami palatinus and hyomandibularis arise, the palatinus containing only communis fibres and running forward in the jugular canal, while the hyomandibularis contains motor, communis and lateralis fibres and runs posteriorly in that canal. The ramus palatinus sends a communicating branch to the general sensory ganglion of the trigeminus, and receives one from the nervus glossopharyngeus. The ramus hyomandibularis receives a general sensory bundle from the trigeminus ganglion, and sends its ramus mandibularis outward anterior to the hyomandibula and its ramus hyoideus outward posterior to that element, between it and a ligament that represents its postfacialis portion.

The nervus glossopharyngeus contains motor, communis and lateralis fibres, and apparently no general sensory ones, and it has a dorsal branch and all the ventral branches typical of a branchial nerve.

The nervus vagus contains motor, general sensory, communis, and lateralis fibres, the latter fibres all entering the ramus supratemporalis vagi and the nervus lineae lateralis. The first and second vagus nerves each has all the typical ventral branches, but in the third nerve these branches are less definitely evident.

Palais de Carnolès,
Menton, France.
Nov. 29*th*, 1921.

LITERATURE CITED

AGASSIZ, L. (1833–1843). *Recherches sur les poissons fossiles.* Neuchâtel.

ALLEN, W. F. (1905). "The Blood Vascular System of the Loricati, the Mail-Cheeked Fishes. *Proc. Wash. Acad. Sci.* vol. VII.

ALLIS, E. P. JR (1889). "The Anatomy and Development of the Lateral Line System of *Amia calva.*" *Journ. Morph.* vol. II.

—— (1897). "The Cranial Muscles, and Cranial and First Spinal Nerves in *Amia calva.*" *Journ. Morph.* vol. XII.

—— (1899). "On certain homologies of the Squamosal, Intercalar, Exoccipitale and Extrascapular bones of *Amia calva.*" *Anat. Anz.* Bd. XVI.

—— (1900*a*). "The Lateral Sensory Canals of *Polypterus bichir.*" *Anat. Anz.* Bd. XVII.

—— (1900*b*). "The Premaxillary and Maxillary Bones, and the Maxillary and Mandibular Breathing Valves of *Polypterus bichir.*" *Anat. Anz.* Bd. XVIII.

—— (1903). "The Skull, and the Cranial and First Spinal Muscles and Nerves in *Scomber scomber.*" *Journ. Morph.* vol. XVIII.

—— (1908*a*). "The Pseudobranchial and Carotid Arteries in *Amiurus.*" *Anat. Anz.* Bd. XXXIII.

—— (1908*b*). "The Pseudobranchial and Carotid Arteries in *Polypterus.*" *Anat. Anz.* Bd. XXXIII.

—— (1909). "The Cranial Anatomy of the Mail-Cheeked Fishes." *Zoologica,* Bd. XXII.

—— (1912). "The Branchial, Pseudobranchial and Carotid Arteries in *Heptanchus* (*Notidanus*) *cinereus.*" *Anat. Anz.* Bd. XLI.

—— (1914). "The Pituitary Fossa and Trigemino-facialis Chamber in Selachians." *Anat. Anz.* Bd. XLVI.

—— (1916). "The so-called Mandibular Artery and the Persisting Remnant of the Mandibular Aortic Arch in the Adult Selachian." *Journ. Morph.* vol. XXVII.

—— (1917). "The Homologies of the Muscles related to the Visceral Arches of the Gnathostome Fishes." *Q.J.M.S.* vol. LXII. Pt. 3.

—— (1918*a*). "The Myodome and Trigemino-facialis Chamber of Fishes and the Corresponding Cavities in Higher Vertebrates." *Proc. Nat. Acad. U.S.A.* vol. IV. No. 8. (An abstract.)

—— (1918*b*). "The Ophthalmic Nerves of the Gnathostome Fishes." *Journ. Compar. Neurol.* vol. XXX.

—— (1918*c*). "On the Origin of the Hyomandibula of the Teleostomi." *Anatom. Rec.* vol. XV.

—— (1919*a*). "The Lips and the Nasal Apertures in the Gnathostome Fishes." *Journ. Morph.* vol. XXXII.

—— (1919*b*). "The Myodome and Trigemino-facialis Chamber of Fishes and the Corresponding Cavities in Higher Vertebrates." *Journ. Morph.* vol. XXXII.

—— (1919*c*). "The Homologies of the Maxillary and Vomer Bones of *Polypterus.*" *Amer. Journ. Anatomy,* vol. XXV.

—— (1919*d*). "The Innervation of the Mandibularis and Geniohyoideus Muscles of the Bony Fishes." *Anatom. Rec.* vol. XVI.

—— (1919*e*). "On the Homologies of the Squamosal Bone of Fishes." *Anatom. Rec.* vol. XVII.

—— (1920*a*). "On Certain Features of the Otic Region of the Chondrocranium of *Lepidosteus,* and Comparison with other Fishes and Higher Vertebrates." *Proc. Zool. Soc.* 1919. London.

—— (1920*b*). "The Branches of the Branchial Nerves of Fishes, with special reference to *Polyodon Spathula.*" *Journ. Compar. Neurol.* vol. XXXII.

—— (1922). "The Myodome and the Trigemino-facialis chamber in the Coelacanthidae, Rhizodontidae and Palaeoniscidae." *In press.*

BAUR, G. (1895). "Ueber die Morphologie des Unterkiefers der Reptilien." *Anat. Anz.* Bd. XI.

BING, R. and BURCKHARDT, R. (1905). "Das Centralnervensystem von *Ceratodus forsteri.*" *Jenaische Denkschriften,* Bd. IV.

BRIDGE, T. W. (1888). "Some Points in the Cranial Anatomy of *Polypterus.*" *Proc. Philos. Soc. Birmingham,* vol. VI.

BRYCE, T. H. (1915). *Quain's Anatomy.* 11th ed. vol. IV, Pt. 1. London.

BUDGETT, J. S. (1902). "On the Structure of the Larval *Polypterus.*" *Trans. Zool. Soc. London,* vol. XVI.

COLLINGE, W. E. (1893). "Note on the Lateral Canal System of *Polypterus*." *Proc. Philos. Soc. Birmingham*, vol. VIII, Pt. 2.

FÜRBRINGER, M. (1897). "Ueber die spino-occipitalen Nerven der Selachier und Holocephalen und ihre vergleichende Morphologie." *Festschrift f. Carl Gegenbaur*, vol. III. Leipzig.

GAUPP, E. (1893). "Primordial-Cranium und Kieferbogen von *Rana fusca*." *Morph. Arbeiten*, Bd. II. Jena.

—— (1905). "Die Entwickelung des Kopfskelets." *Handbuch d. vergl. u. experim. Entwickelungslehre d. Wirbeltiere*, von Oscar Hertwig, 1906, Bd. III, Th. 2.

GEGENBAUR, C. (1872). *Das Kopfskelet der Selachier: Untersuchungen zur vergleichenden Anatomie der Wirbeltiere*, Hft 3. Leipzig.

—— (1878). "Ueber das Kopfskelet von *Alepocephalus rostratus*." *Morph. Jahrb.* Bd. IV. Sup.

HERRICK, C. J. (1899). "The Cranial and First Spinal Nerves of Menidia: A Contribution upon the Nerve Components of the Bony Fishes." *Journ. Comp. Neurol.* vol. IX.

HOLMQVIST, O. (1910). "Der Musculus Protractor Hyoidei und der Senkungsmechanismus des Unterkiefers bei den Knochenfischen." *Lunds Universitets Arsskrift*, N.F. Afd. 2, Bd. VI, Nr. 6. Lund.

—— (1911). "Studien in der von den NN. Trigeminus und Facialis innervierten Muskulatur der Knochenfische." *Lunds Universitets Arsskrift*, N.F. Afd. 2, Bd. VII, Nr. 7. Lund.

HUXLEY, T. H. (1861). "Preliminary Essay upon the Systematic Arrangement of the Fishes of the Devonian Epoch." *Memoir Geol. Survey of United Kindom*, Decade 10. London.

JAQUET, M. (1898). "Recherches sur l'anatomie et l'histologie du *Silurus glanis*, L." *Arch. d. Sciences Médicales*, Tome III. Paris.

JOHNSTON, J. B. (1911). "The telencephalon of Ganoids and Teleosts." *Journ. Comp. Neurol.* vol. XXI, No. 6.

KERR, J. G. (1907). "The Development of *Polypterus*." *Proc. Royal Physical Soc. Edinburgh*, vol. XVII, No. 2.

KINDRED, J. E. (1919). "The Skull of *Amiurus*." *Illinois Biol. Monographs*, vol. V, No. 1.

LEHN, CHARLOTTE (1918). "Beitrag zur Kenntnis des Primordialschädels von *Polypterus*." *Zeitsch. f. angewandte Anat. u. Konstitutionslehre*, Bd. II, Hft. 4–6.

LUTHER, A. (1913). "Ueber die vom N. trigeminus versorgte Muskulatur der Ganoiden und Dipneusten." *Acta Soc. Sc. Fenn.* Tome XLI, No 9.

MÜLLER, J. (1846). *Ueber den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische*. Berlin.

NORRIS, H. W. (1908). "The Cranial Nerves of *Amphiuma means*." *Journ. Comp. Neurol.* vol. XVIII.

NOWIKOFF, M. (1909). "Untersuchungen über die Structur des Knochens." *Zeit. Wiss. Zoologie*, Bd. XCII.

PARKER, W. K. (1873). "On the Structure and Development of the Skull in Salmon (*Salmo salar*, L.)." *Phil. Trans Royal Soc. London*, vol. CLXIII.

POLLARD, H. B. (1891). "On the Anatomy and Phylogenetic Position of *Polypterus*." *Anat. Anz.* Bd. VI.

—— (1892). "On the Anatomy and Phylogenetic Position of *Polypterus*." *Zool. Jahrb. Abt. f. Anat. u. Ontog. d. Thiere*, Bd. V.

RETZIUS, G. (1881). *Biologische Untersuchungen*. IV. Das Membranöse Gehörorgan von *Polypterus bichir*. Geoffr. und *Calamoichthys calabricus*, J. A. Smith. Stockholm.

SAGEMEHL, M. (1884). "Beiträge zur vergleichenden Anatomie der Fische. III. Das Cranium der Characiniden nebst allgemeinen Bemerkungen über die mit einem Weber'schen Apparat versehenen Physostomen Familien." *Morph. Jahrb.* Bd. X.

—— (1891). "Beiträge zur vergleichenden Anatomie der Fische. IV. Das Cranium der Cyprinoiden." *Morph. Jahrb.* Bd. XVII.

SCHÄFER, E. A. (1893). *Quain's Elements of Anatomy*, vol. I, Pt. 2. 10th ed. London.

SCHAUINSLAND, H. (1906). "Die Entwickelung der Wirbelsäule nebst Rippen und Brustbein." *Handbuch d. vergl. u. experim. Entwickelungslehre d. Wirbeltiere*, von Oscar Hertwig. Bd. III, Abth. 2.

SEWERTZOFF, A. N. (1899). "Die Entwickelung des Selachierschädels. Ein Beitrag zur Theorie der correlativen Entwickelung." *Festschrift C. von Kupffer*.

SEWERTZOFF, A. N. (1911). "Die Kiemenbogennerven der Fische." *Anat. Anz.* Bd. XXXVIII.

SONIES, F. (1907). *Ueber die Entwickelung des Chondrocraniums und der knorpeligen Wirbelsäule bei den Vögeln.* Petrus Camper. Deel IV.

STENSIÖ, E. A. (1921). *Triassic Fishes from Spitzbergen*, Part 1. Adolf Holzhausen. Vienna.

TRAQUAIR, R. H. (1871). "On the Cranial Osteology of *Polypterus*." *Journ. Anat. and Phys.* vol. v. London.

WALDSCHMIDT, J. (1887). "Beitrag zur Anatomie des Centralnervensystems und des Geruchsorgans von *Polypterus bichir*." *Anat. Anz.* Bd. II.

WIEDERSHEIM, R. (1904). "Ueber das Vorkommen eines Kehlkopfes bei Ganoiden und Dipnoern sowie über die Phylogenie der Lunge." *Zool. Jahrb.* Sup. Bd. VII.

—— (1906). *Grundriss der Vergleichenden Anatomie der Wirbeltiere.* Jena.

WIJHE, J. W. VAN (1882). "Ueber das Visceralskelet und die Nerven des Kopfes der Ganoiden und von *Ceratodus*." *Niederl. Arch. f. Zool.* Bd. v.

WINSLOW, G. M. (1898). "The Chondrocranium in the Ichthyopsida." *Tufts College Studies*, No. 5.

ABBREVIATIONS IN PLATES

aa$^{1-4}$, afferent arteries of first to fourth branchial arches; *ab*, nervus abducens; *abfr*, foramen for nervus abducens; *ac*, aortic canal; *A.HM*, accessory hyomandibula; *ah*, afferent artery of hyal arch; *Am*^{1}, superficial division of musculus adductor mandibulae; *Am*^{2}, deeper division of musculus adductor mandibulae; *Am*^{3}, mandibular division of musculus adductor mandibulae; *ANA*, accessory nasal; *Ao*, musculus adductor operculi; *ART*^{a}, autarticular; *ART*^{d}, dermarticular; *AUP*, autopalatine; *ba*, bulla acustica; *BB*, basibranchial; *BEO*, basi-exoccipital; *Bm*, musculus branchiomandibularis; *CB*$^{1-5}$, ceratobranchials of first to fifth arches; *cf*, canal for nervus hyomandibularis facialis; *CH*, ceratohyal; *cj*, canal for vena jugularis; *cl*, ramus ciliaris longus; *CP*, cheek plate; *cpf*, canal for ramus palatinus facialis; *D*, dentary; *dl*, dorsal body-line of pit organs; *Do*, musculus dilatator operculi; *EB*^{1}, epibranchial of first branchial arch; *ECP*, ectopterygoid; *ECT*, ectethmoid; *eg*, antero-mesial ectethmoidal groove; *EH*, epihyal; *ENP*, entopterygoid; *ETH*, ethmoid; *ffr*, foramen for nervus facialis; *Ghi*, musculus geniohyoideus inferior; *Ghs*, musculus geniohyoideus superior; *glfr*, foramen for nervus glossopharyngeus; *HB*$^{1-2}$, hypobranchials of first and second branchial arches; *hf*, ramus hyoideus facialis; *HH*, hypohyal; *Hhi*, musculus hyohyoideus inferior; *Hhs*, musculus hyohyoideus superior; *HM*, hyomandibula; *il*, intermediate body-line of pit organs; *ioc*, infraorbital latero-sensory canal; *ip*$^{1-11}$, pores of infraorbital line; i^2s^2p, double pore at point of union of supraorbital and infraorbital canals; $i^{10}s^7p$, double pore at point of union of supraorbital and infraorbital canals; *Iv*$^{1-4}$, musculi interarcuales ventrales; *LA*, lachrymal; *Lab*$^{1-5}$, levator muscles of first to fifth arches; *Lap*, musculus levator arcus palatini; *ll*, lateral line of body; *M*, Meckel's cartilage; *MDP*, mesial dermopalatini; *mdt*, ramus mandibularis trigemini; *mef*, ramus mandibularis externus facialis; *mf*, ramus mandibularis facialis; *mif*, ramus mandibularis internus facialis; *MM*, mentomeckelian ossicle; *MP*, metapterygoid; *MX*, maxillary; *mxt*, ramus maxillaris trigemini; *NA*, nasal; *nll*, nervus lineae lateralis; *nt*, nasal tube; *o*, nervus opticus; *ocfr*, foramen for oculomotorius and ophthalmicus profundus; *ocm*, nervus oculomotorius; *ofr*, foramen for nervus opticus and internal carotid artery; *oi*, musculus obliquus inferior; *onfr*, foramen for orbito-nasal artery; *opf*, ramus opercularis facialis; *opp*, nervus ophthalmicus profundus; *OPS*, opisthotic; *opt*, ramus ophthalmicus trigemini; *os*, musculus obliquus superior; *OT*, Os terminale; *otfr*, foramen for ramus ophthalmicus trigemini; *PA*, parieto-dermopterotic; *PB*^{1}, pharyngobranchial of first branchial arch; *Pc*, musculus pharyngo-clavicularis; *pfr*, foramen for pituitary vein; *Pg*, musculus pterygoideus; *Ph*, musculus protractor hyomandibularis; *pmp*, preoperculo-mandibular pores; *PMX*, premaxillary; *pna*, posterior nasal aperture; *pq*, palatoquadrate; *PS*, parasphenoid; *PSF*, postfronto-sphenotic; *PT*, posttemporal; *Q*, quadrate; *re*, musculus rectus externus; *rif*, musculus rectus inferior; *rit*, musculus rectus internus; *rs*, musculus rectus superior; *s*, spiracle; *Sh*, musculus sternohyoideus; *SP*, sphenoid; *Sp*, musculus spiracularis; *sp*$^{1-6}$, pores of supraorbital canal; *SPL*, splenial; *ST*, supratemporals; *ta*, truncus arteriosus; *tfr*, foramen for nervus trigeminus; *Tp*, musculus temporalis; *trfr*, foramen for nervus trochlearis; *Tv*, musculus transversus ventralis; *vfr*, foramen for nervus vagus.

Fig. 1a

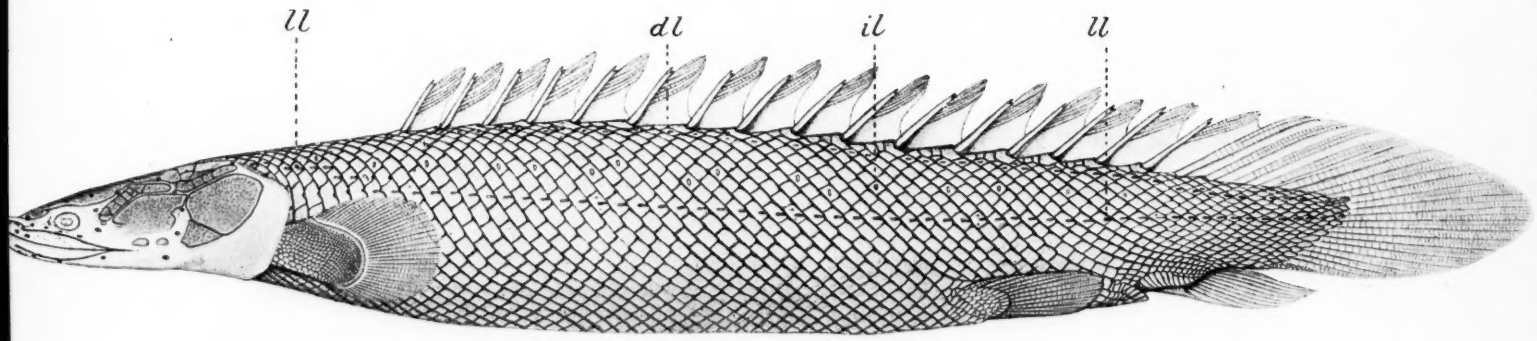


Fig. 1

Fig. 1b

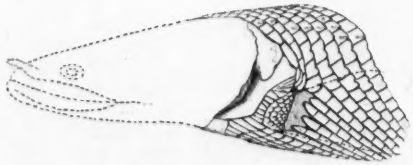


Fig. 1c

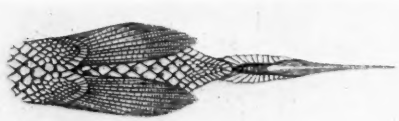


Fig. 1. Full length lateral view of 44 cm. *Polypterus bichir*. ×1.
Fig. 1*a*. Dorsal view of mid-dorsal line of same. ×1.
Fig. 1*b*. Lateral view of anterior portion of trunk of same, with pectoral fin removed. ×1.
Fig. 1*c*. Ventral view of anal fins of same. ×1.

UNIV. OF MICH.

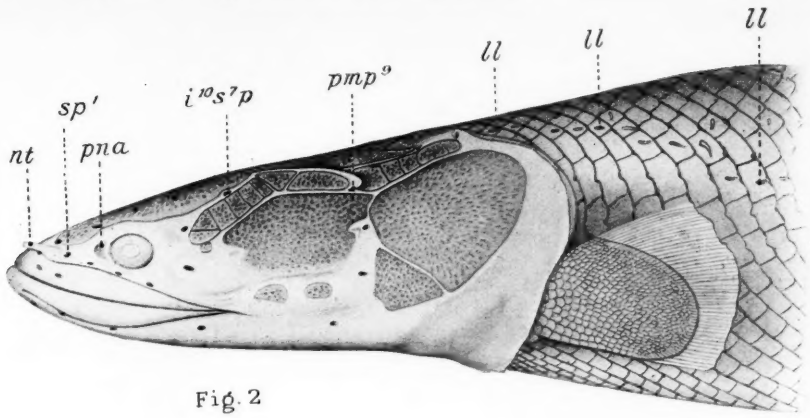


Fig. 2

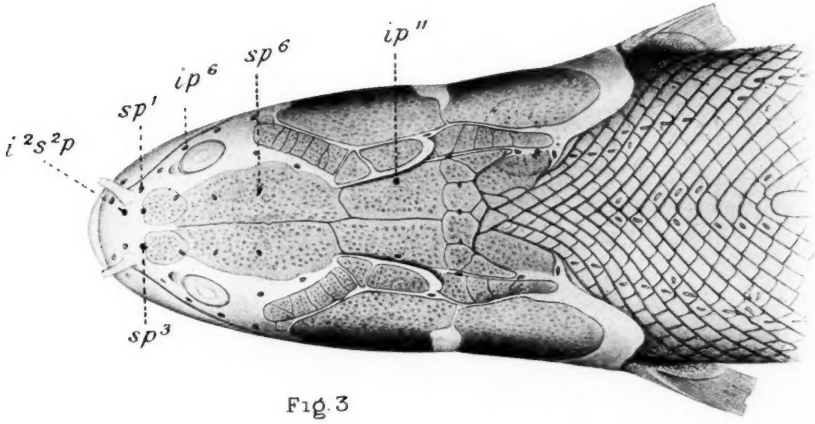


Fig. 3

Fig. 4

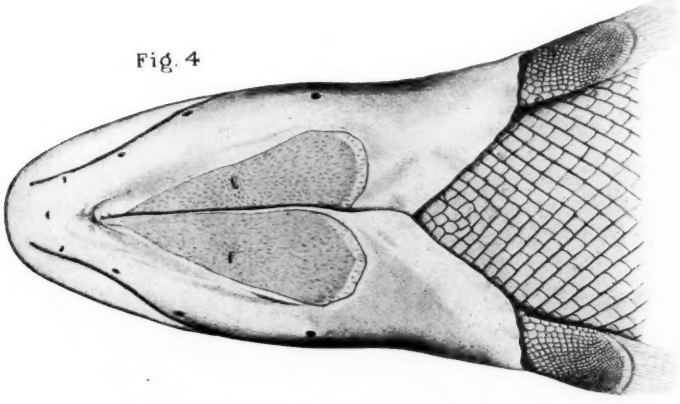


Fig. 2. Lateral view of head of 44 cm. *Polypterus bichir.* ×2.
Fig. 3. Dorsal view of head of same. ×2.
Fig. 4. Ventral view of head of same. ×2.

UNIV. OF MICH.

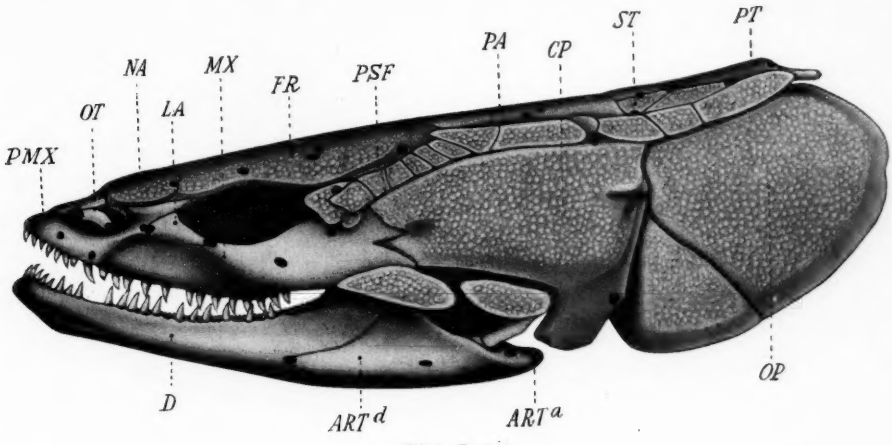


Fig. 5

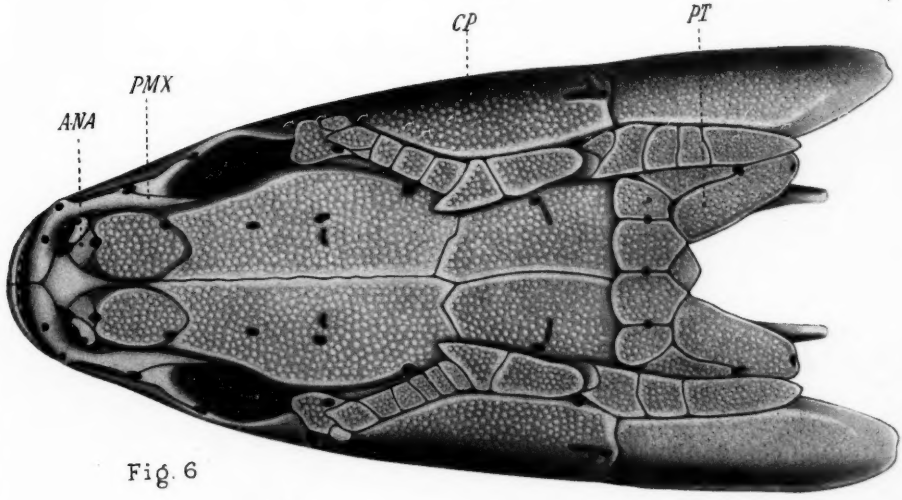
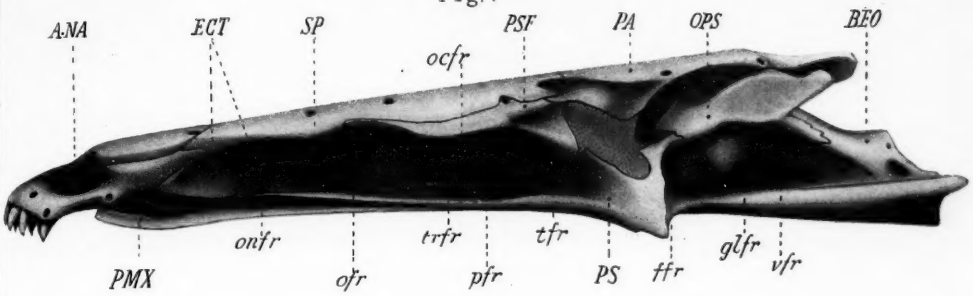


Fig. 6

Fig. 5. Lateral view of entire skull of a 49 cm. *Polypterus bichir.* ×2.
Fig. 6. Dorsal view of same. ×2.

UNIV OF MICH.

Fig. 7



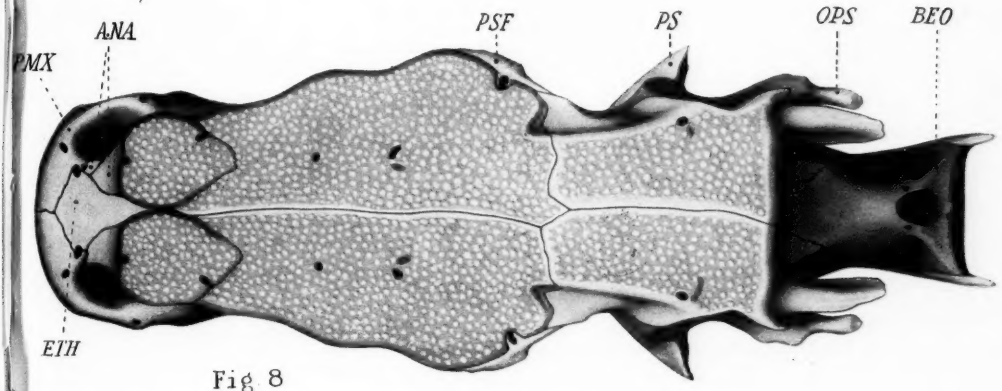


Fig 8

Fig. 9

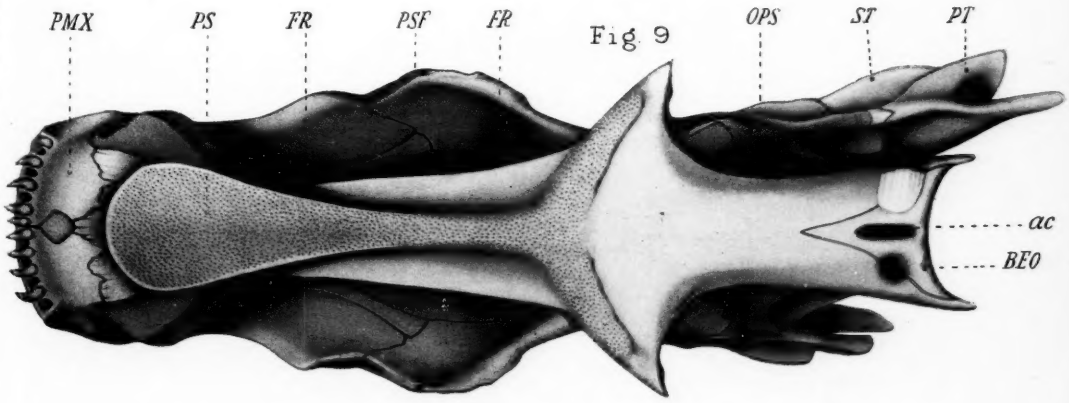


Fig. 7. Lateral view of neurocranium of large specimen of *Polypterus bichir* from Abyssinia. ×2.
Fig. 8. Dorsal view of same. ×2.
Fig. 9. Ventral view of same. ×2.

UNIV. OF MICH.

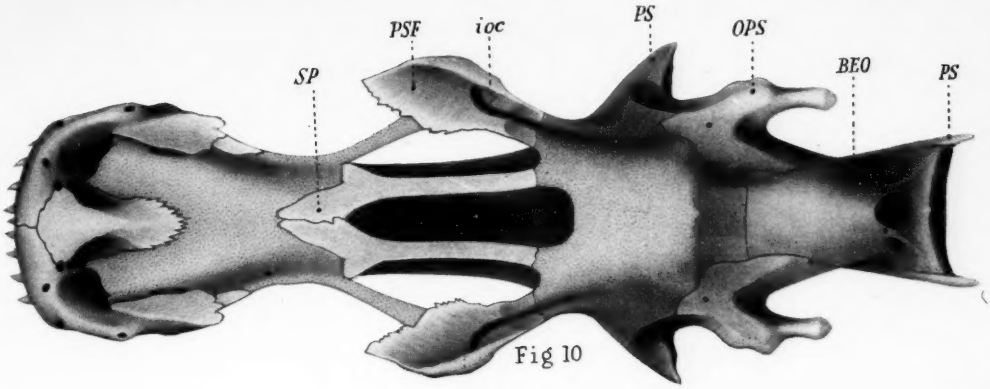


Fig 10

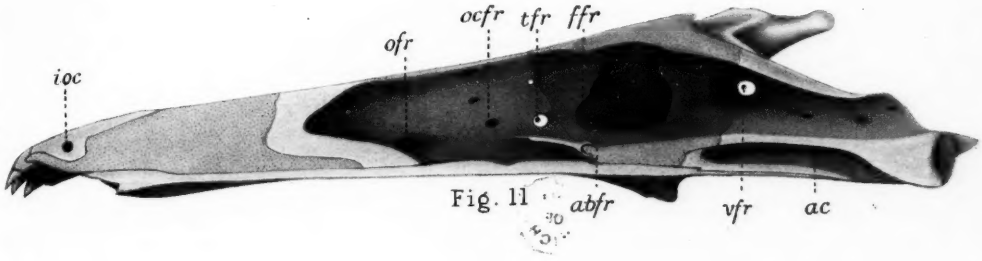


Fig. 11

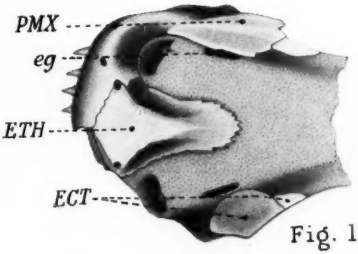


Fig. 12

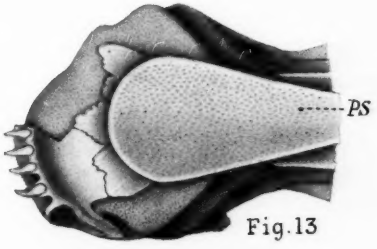


Fig. 13

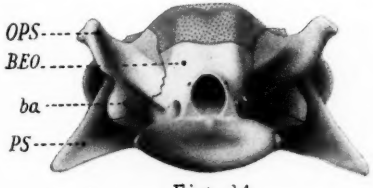


Fig. 14

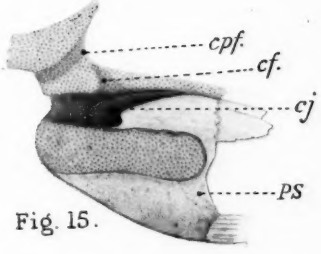


Fig. 15.

Fig. 10. Dorsal view of neurocranium of large specimen of *Polypterus bichir* from Abyssinia with dermal bones removed. ×2.
Fig. 11. Median view of bisected skull of same. ×2.
Fig. 12. Dorsal view of ethmoidal region of same, with left premaxillary removed. ×2.
Fig. 13. Ventral view of same. ×2.
Fig. 14. Posterior view of neurocranium of same. ×2.
Fig. 15. Dorsal view of section through jugular canal. ×3.

UNIV. OF MICH.

Fig. 16

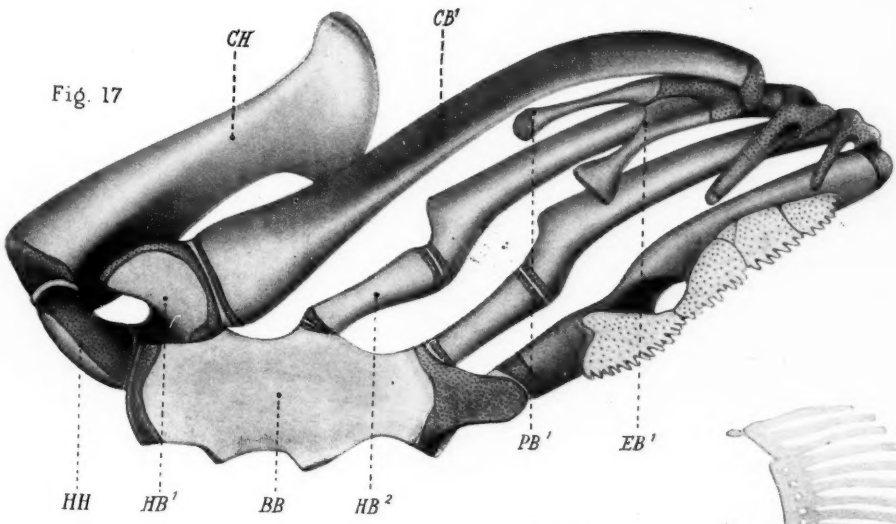


Fig. 17

Fig. 18.

Fig. 20

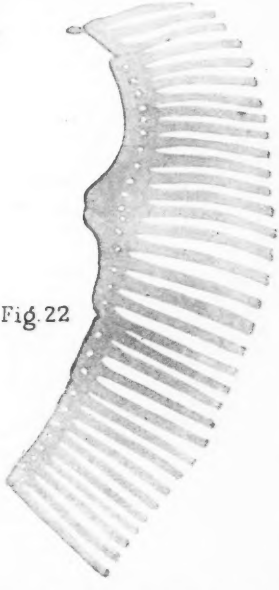


Fig. 22

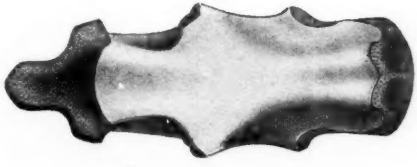
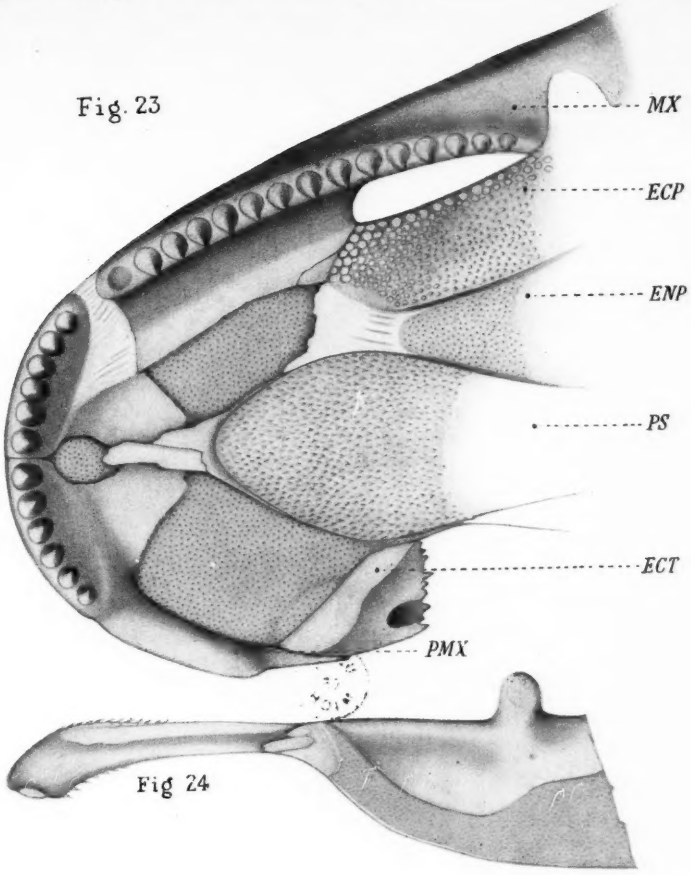


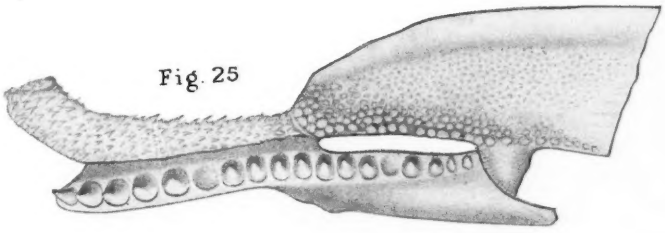
Fig. 19

Fig. 21.

Fig. 16. Ventral view of hyal and branchial arches of large specimen of *Polypterus bichir* from Abyssinia. ×2. Fig. 17. Dorsal view of same. ×2. Fig. 18. Lateral view (right side) of basibranchial of same. ×2. Fig. 19. Ventral view of same. ×2. Fig. 20. Ventral view of first hypobranchial of same. ×2. Fig. 21. Dorsal view of same. ×2. Fig. 22. Lateral view of branchial rays of second branchial arch. ×4.

UNIV. OF MICH.





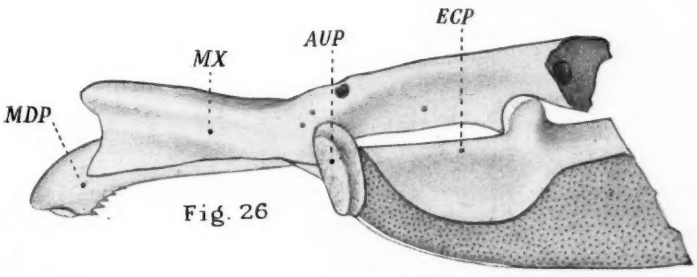


Fig. 23. Ventral view of anterior portion of roof of mouth of a 27 cm. specimen of *Polypterus Lapradei*, with right maxillary bone and both median dermopalatines removed. ×6.
Fig. 24. Dorsal view of right median dermopalatine and anterior end of palatoquadrate. ×6.
Fig. 25. Ventral view of same, with maxillary attached. ×6.

UNIV. OF MICH.

F

Fig.

Fig. 27

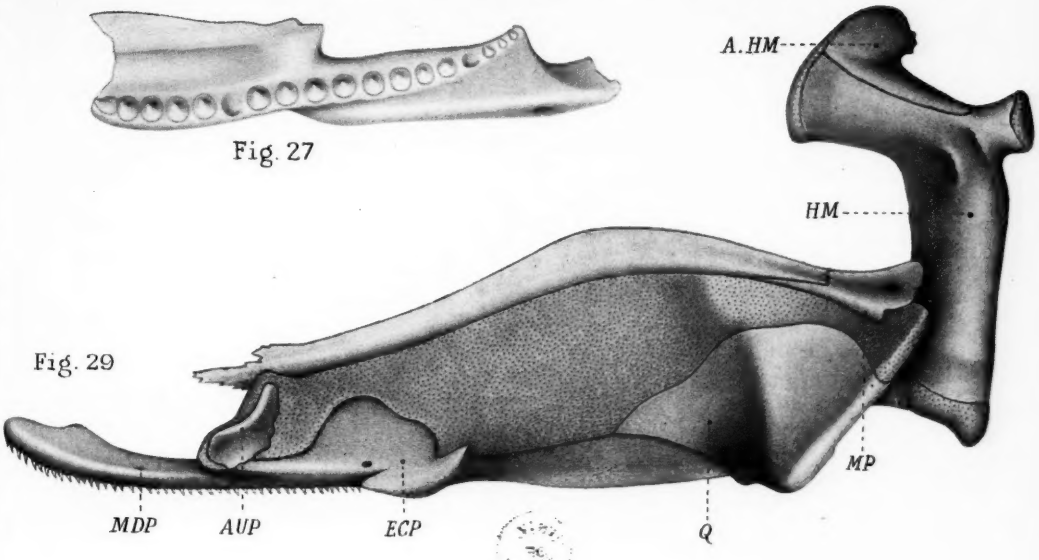


Fig. 29

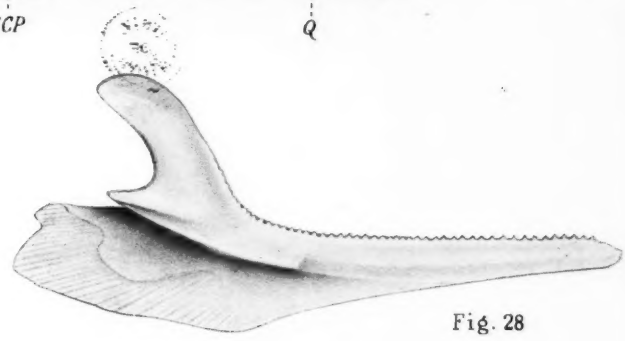


Fig. 28

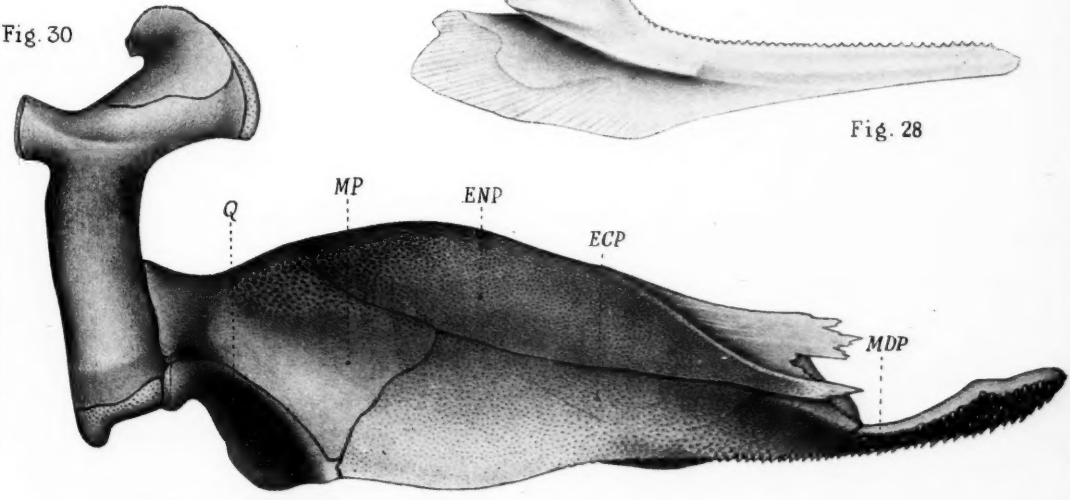
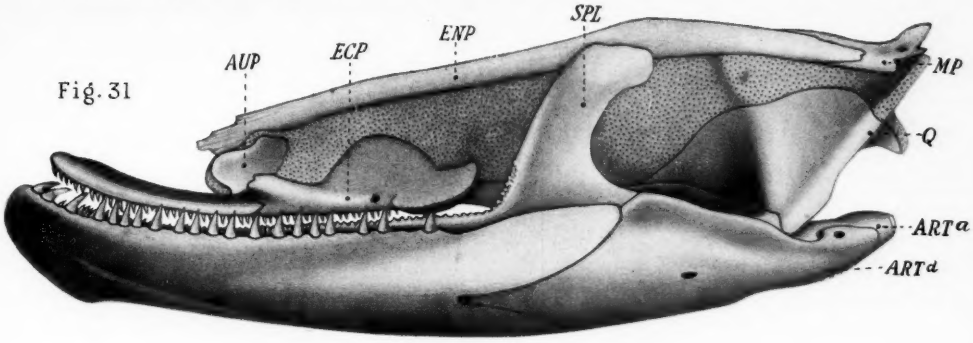


Fig. 30

Fig. 27. Ventral view of right maxillary of a 27 cm. specimen of *Polypterus Lapradei*. ×6.
Fig. 28. Lateral view of splenial of large specimen of *Polypterus bichir* from Abyssinia. ×2.
Fig. 29. Lateral view of hyomandibula and palatoquadrate of same. ×2.
Fig. 30. Median view of same. ×2.

UNIV. OF MICH.

Fig. 31



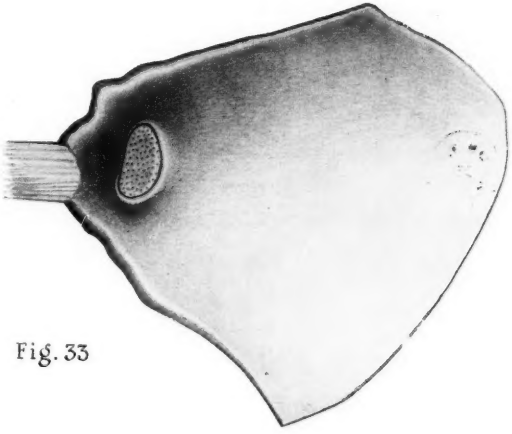


Fig. 33

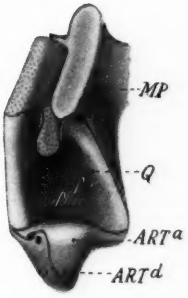


Fig. 32

Fig. 34

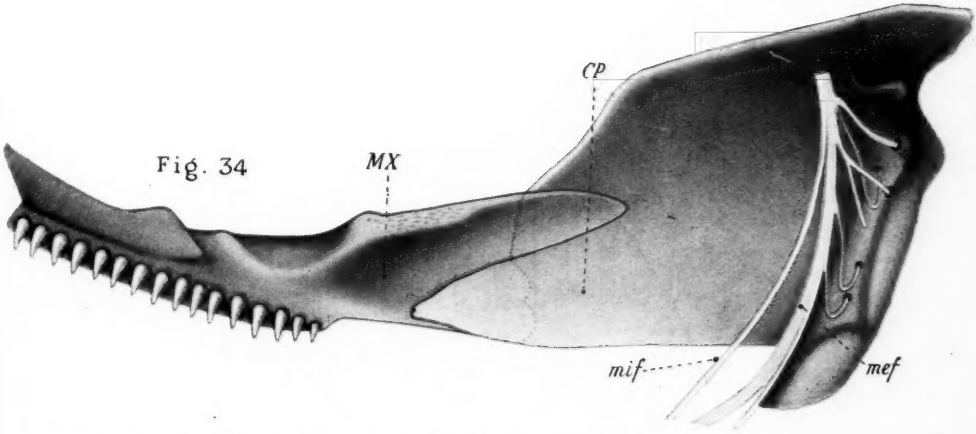


Fig. 31. Lateral view of palatoquadrate and mandible of large specimen of *Polypterus bichir* from Abyssinia. × 2.
Fig. 32. Posterior view of same. ×2.
Fig. 33. Internal view of operculum of same specimen. ×2.
Fig. 34. Internal view of cheek-plate and maxillary of same specimen. ×2.

UNIV. OF MICH.

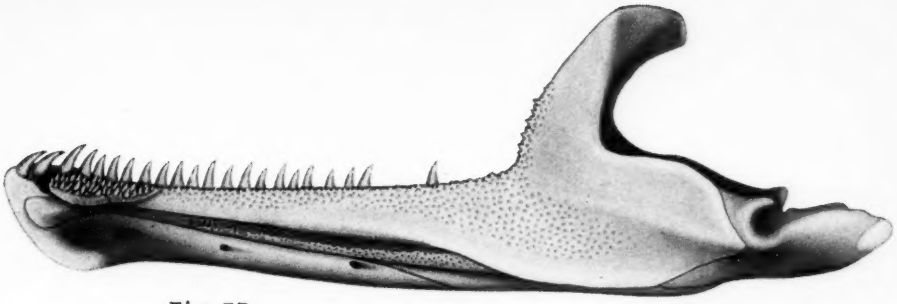


Fig. 35

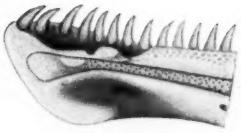
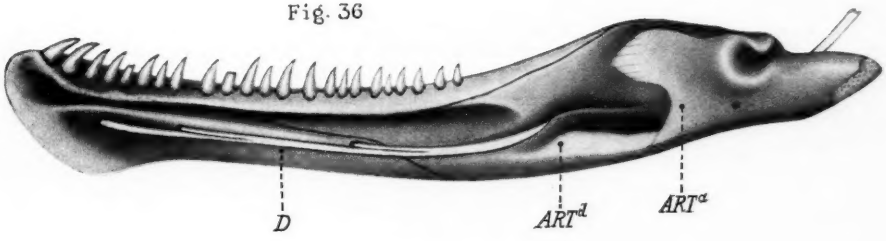


Fig. 35*a*

Fig. 39

Fig. 38

Fig. 36



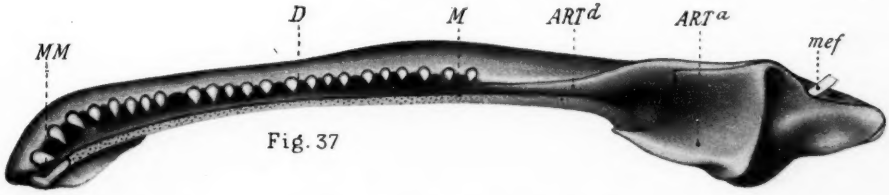


Fig. 37

Fig. 35. Internal view of left mandible of large specimen of *Polypterus bichir* from Abyssinia. ×2.
Fig. 35*a*. Anterior end of the same with dermal ossicles removed. ×2.
Fig. 36. The same with splenial removed. ×2.
Fig. 37. Dorsal view of the same. ×2.
Fig. 38. Dorso-mesial view of the autarticular. ×2.
Fig. 39. Lateral view of the same. ×2.

UNIV. OF MICH.

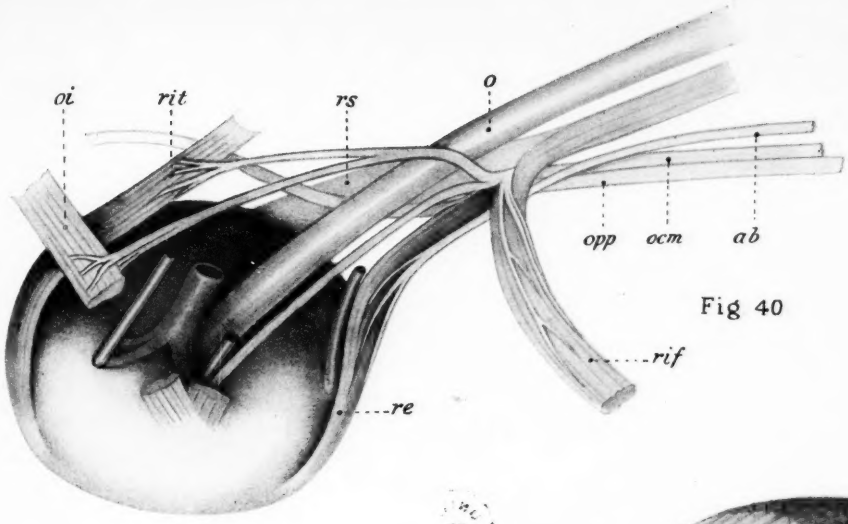


Fig 40

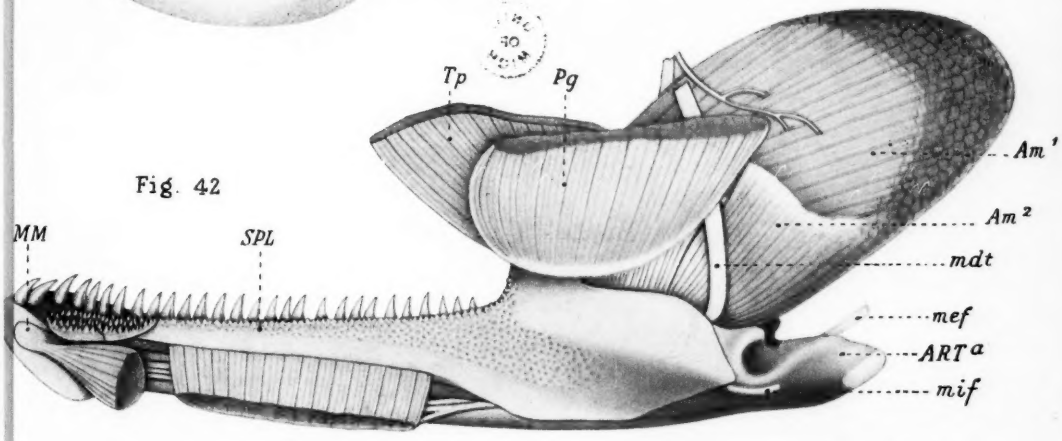


Fig. 42

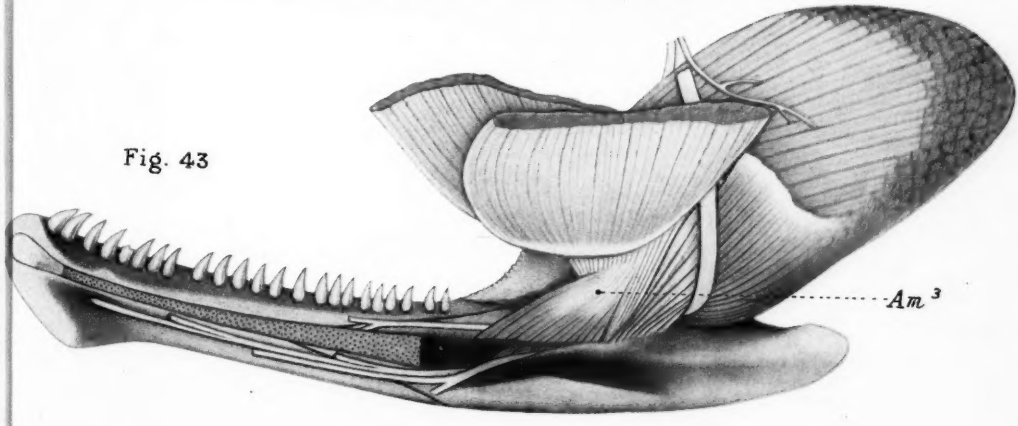


Fig. 43

Fig. 40. Ventral view of right eyeball of large specimen of *Polypterus bichir* from Abyssinia. ×6.
Fig. 42. Internal view of mandible with muscles attached. ×2.
Fig. 43. The same, with splenial removed. ×2.

UNIV. OF MICH.

Fig. 41

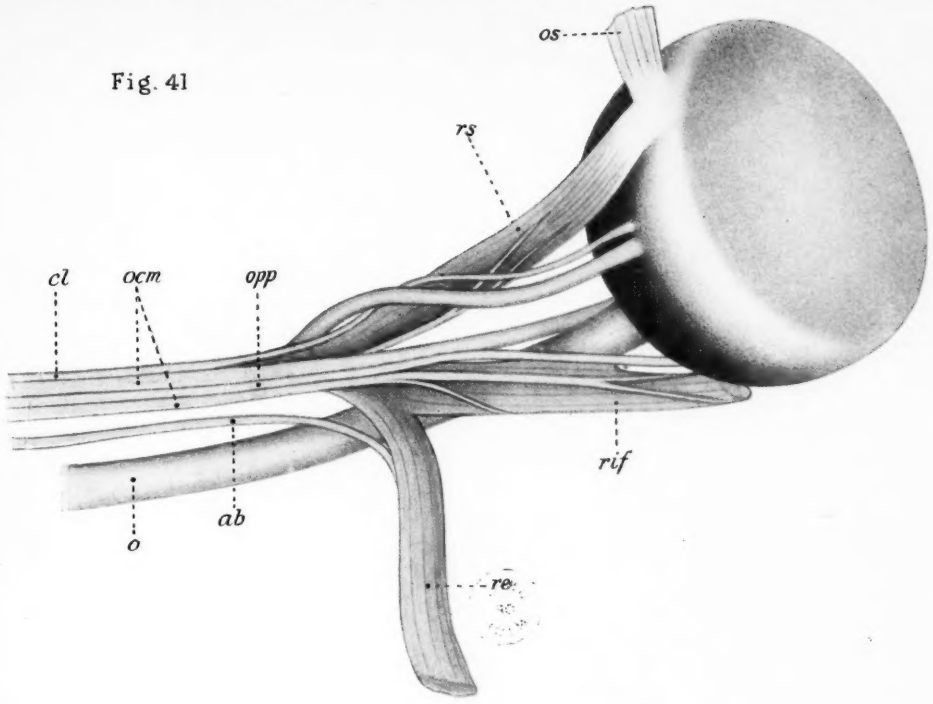


Fig. 44 *a*

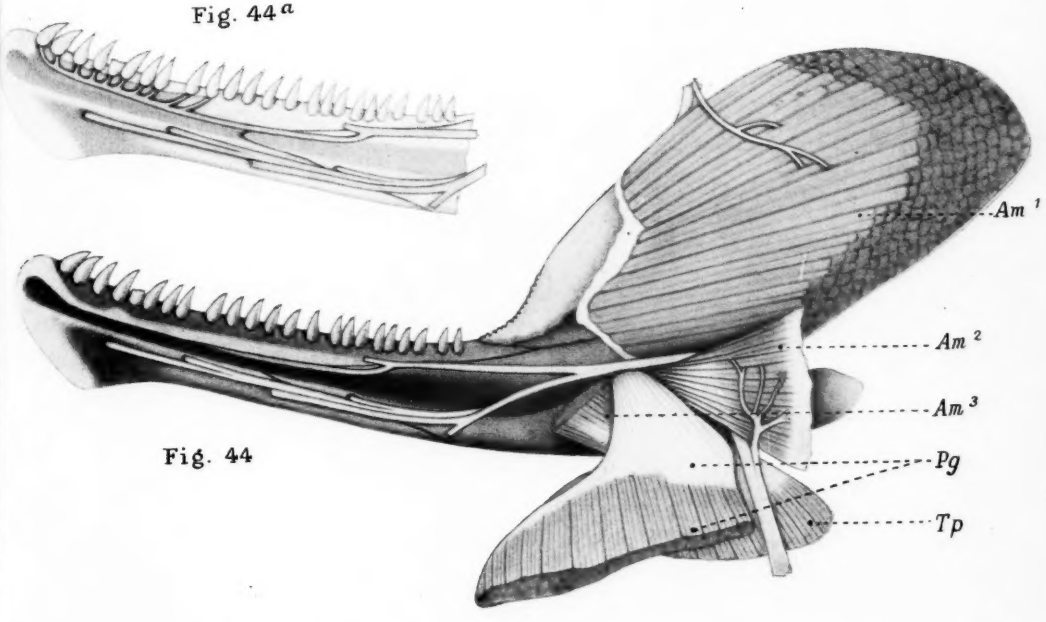


Fig. 44

Fig. 41. Lateral view of right eyeball of large specimen of *Polypterus bichir* from Abyssinia. ×6.
Fig. 44. Internal view of mandible with musculi temporalis and pterygoideus turned downward. ×2.
Fig. 44*a*. Anterior end of the same, showing innervation of the teeth. ×2.

UNIV. OF MICH.

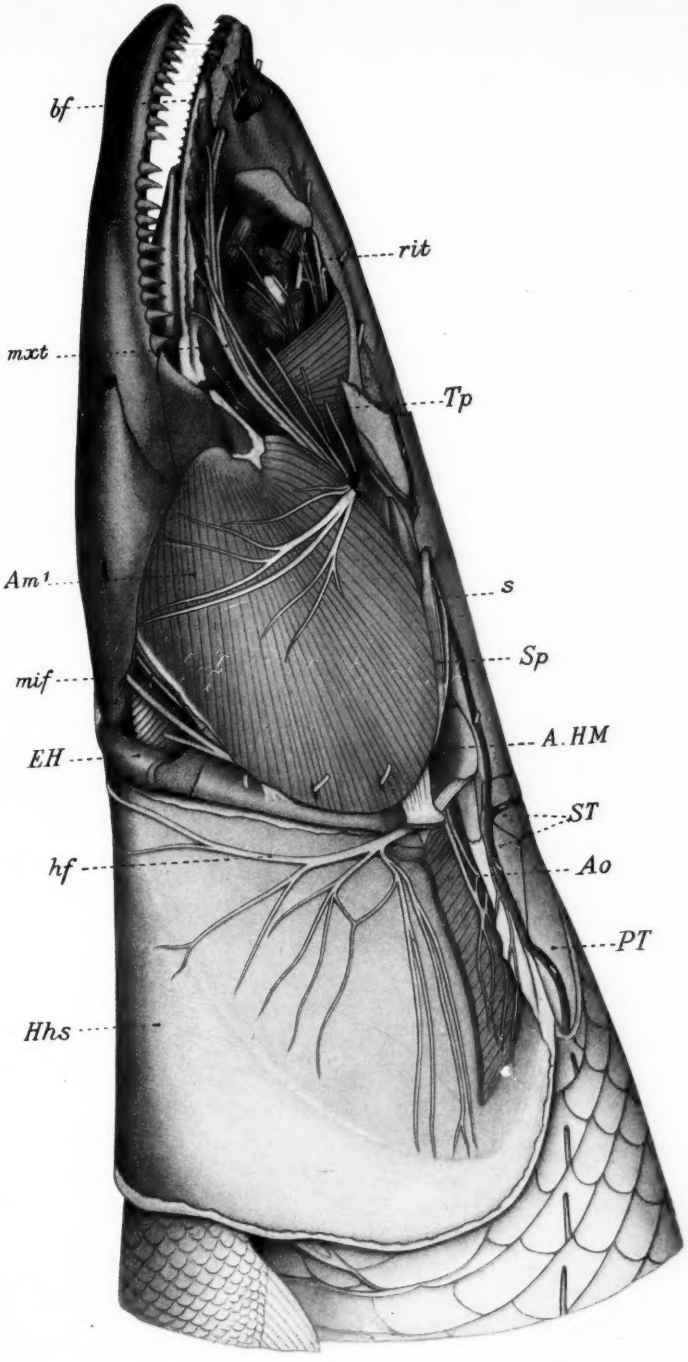


Fig. 45. Lateral view of head of large *Polypterus bichir* from Abyssinia, with skin and eyeball removed. ×2.

UNIV. OF MICH.

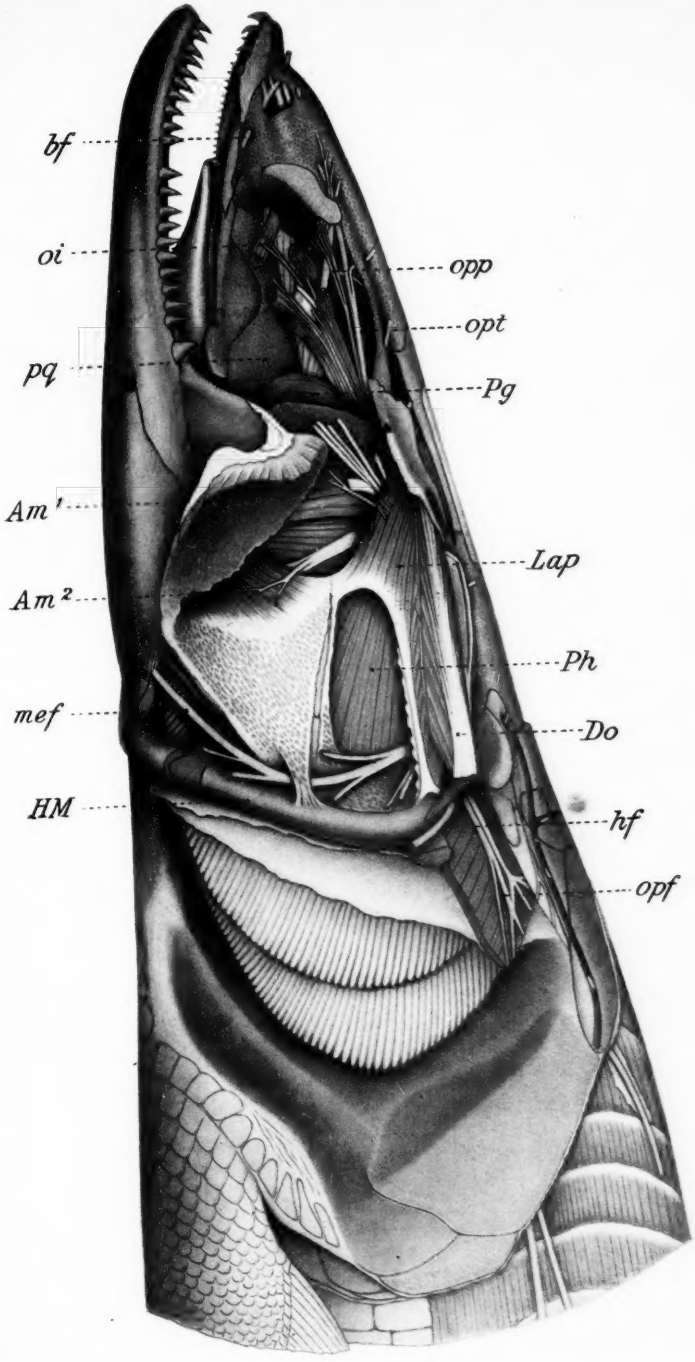


Fig. 46. Lateral view of head of large *Polypterus bichir* from Abyssinia, with musculus masseter removed. × 2.

UNIV. OF MICH.

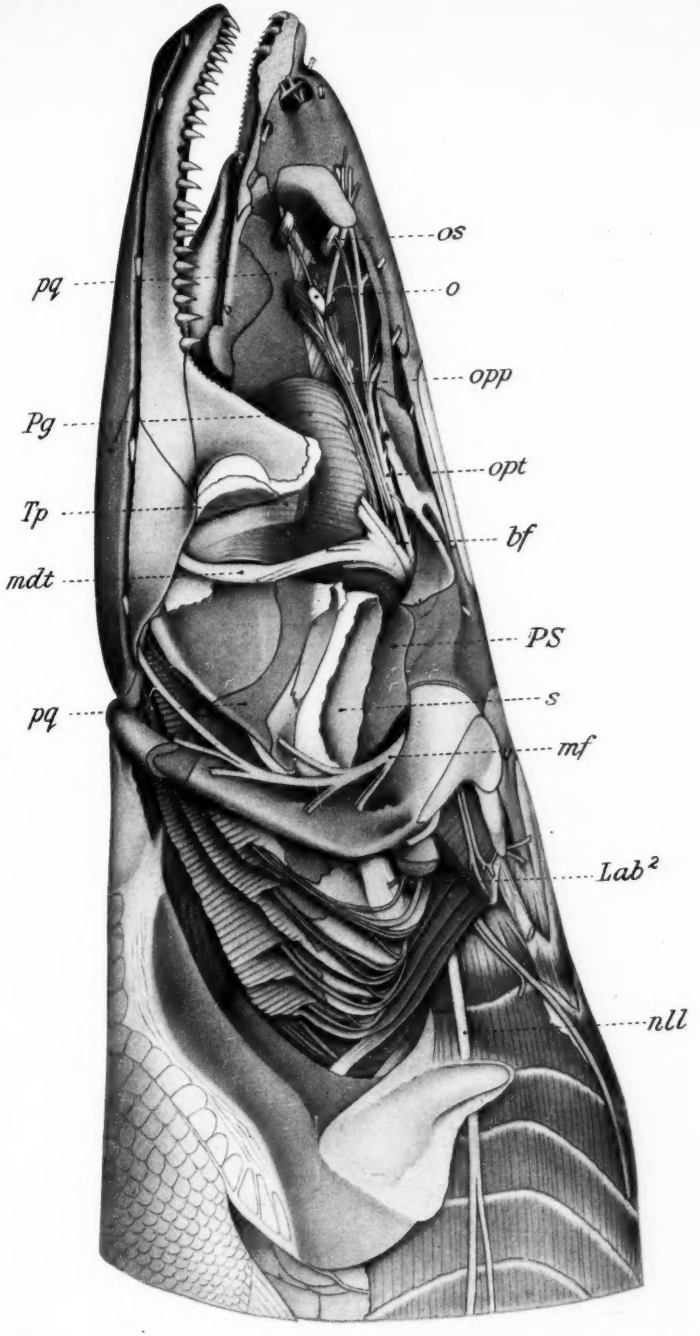


Fig. 47. A deeper dissection of head of large *Polypterus bichir* from Abyssinia. × 2.

UNIV. OF MICH.

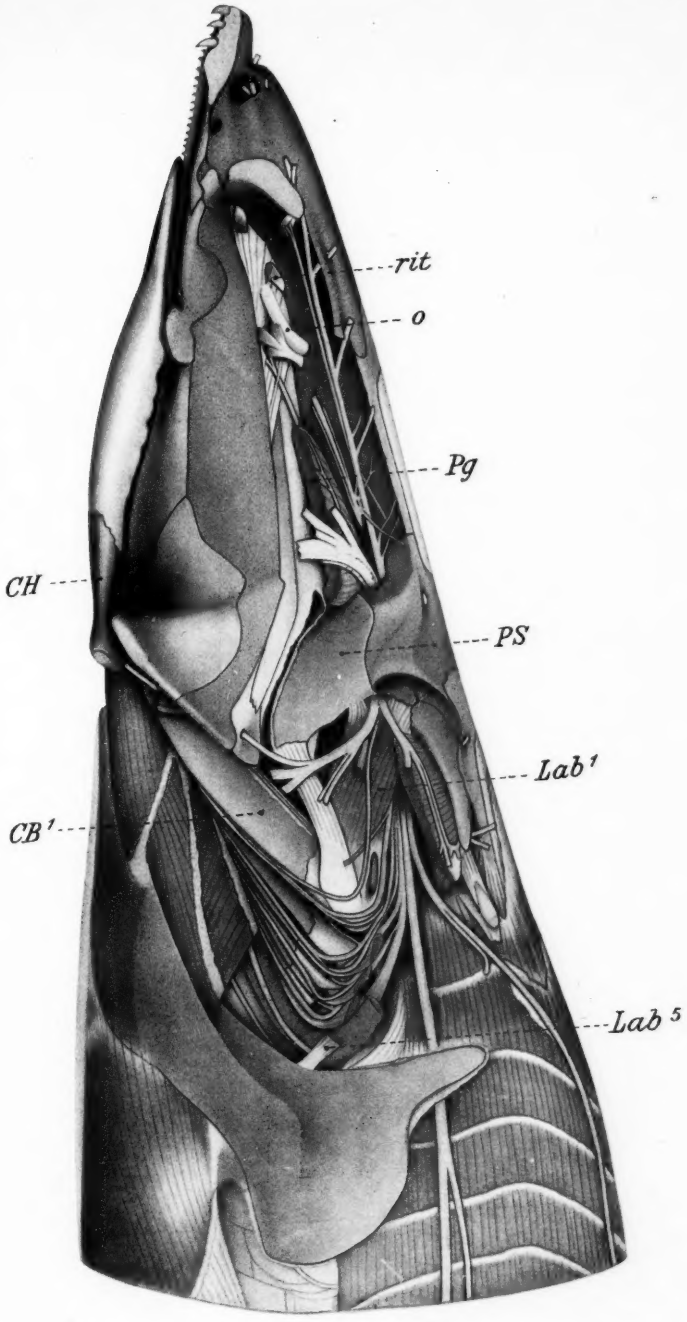


Fig. 48. A still deeper dissection of head of large *Polypterus bichir* from Abyssinia. × 2.

UNIV. OF MICH.

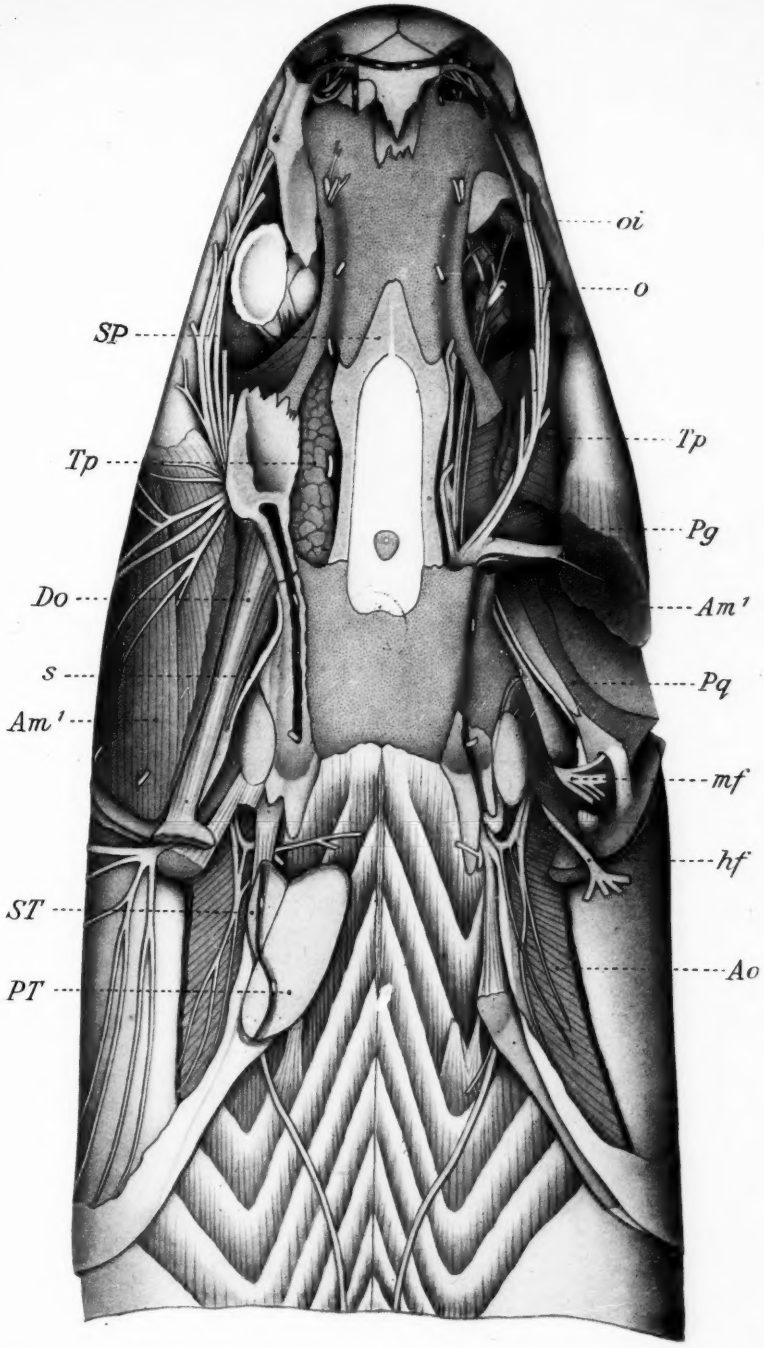


Fig. 49. Dorsal view of head of large *Polypterus bichir* from Abyssinia, with skin and dermal bones removed. × 2.

UNIV. OF MICH.

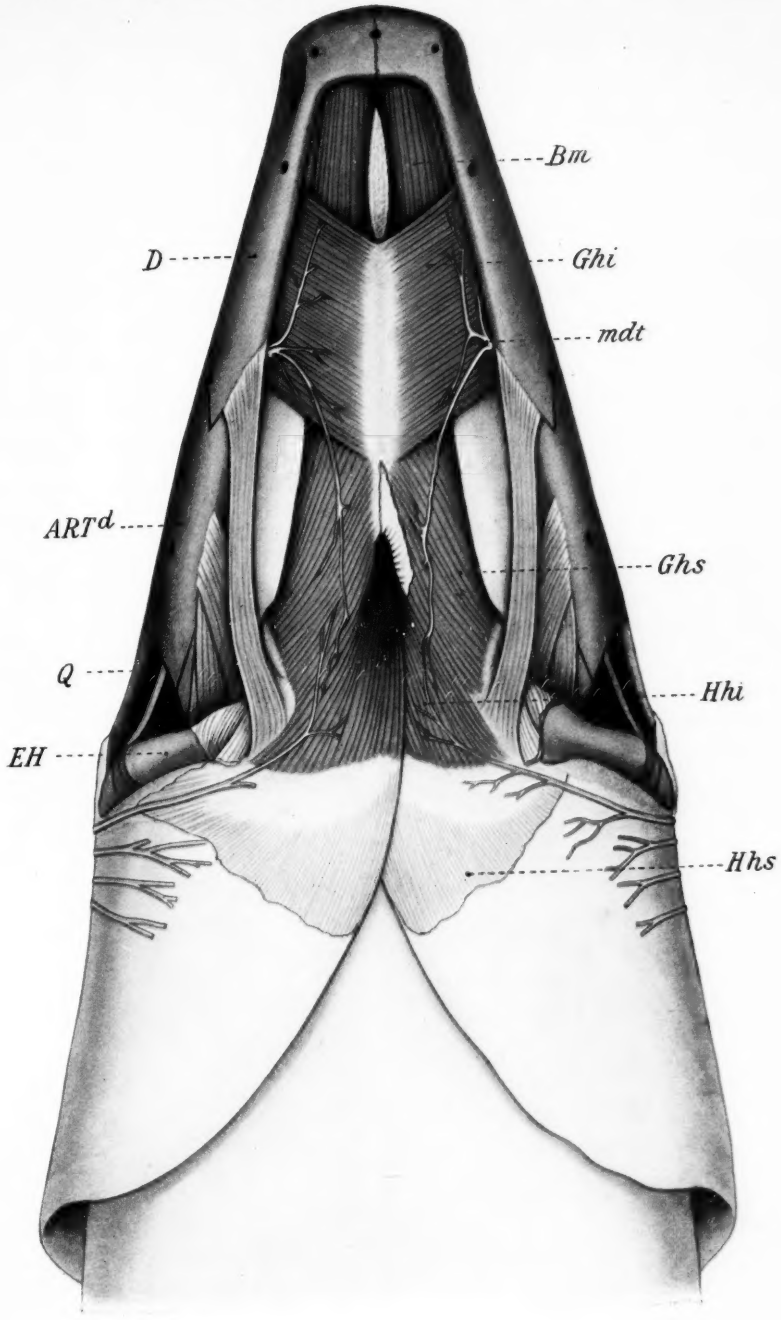


Fig. 50. Ventral view of a second head of large *Polypterus bichir*, with skin removed. × 2.

UNIV. OF MICH.

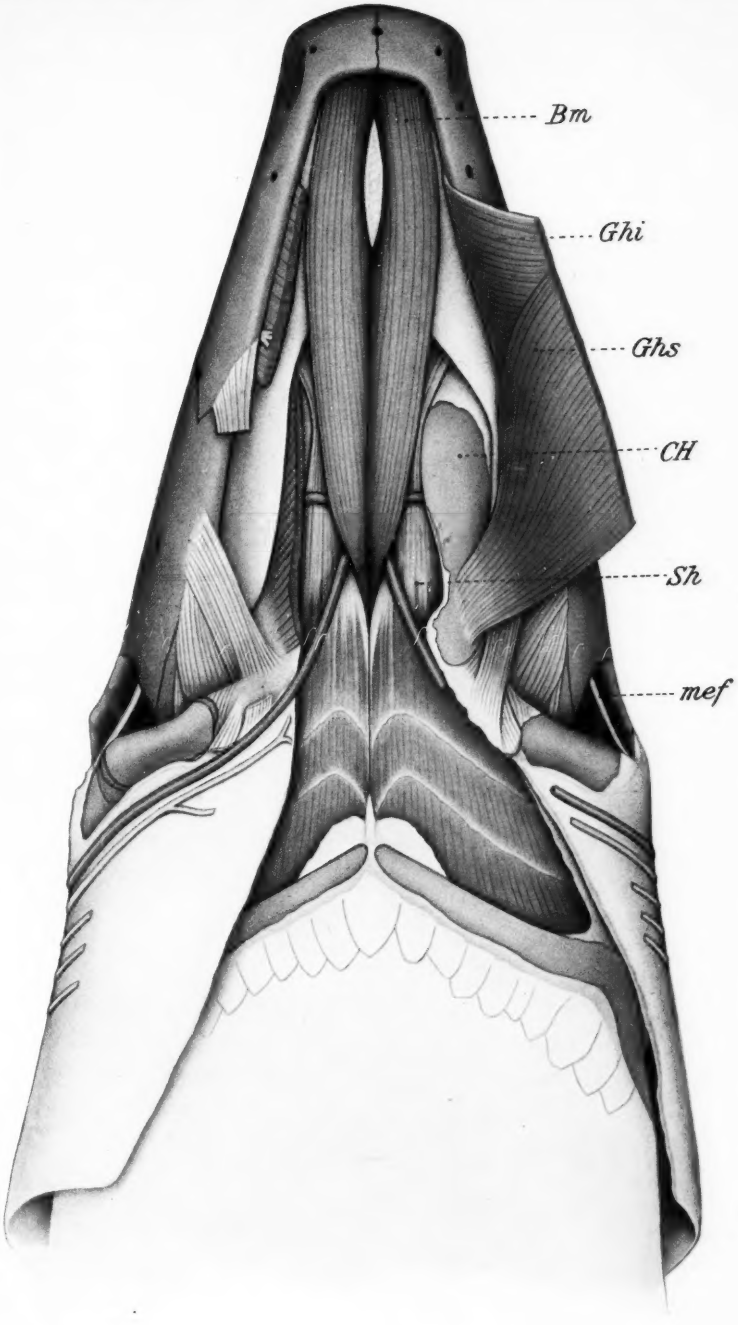


Fig. 51. A deeper dissection of a second head of large *Polypterus bichir*. ×2.

UNIV. OF MICH.

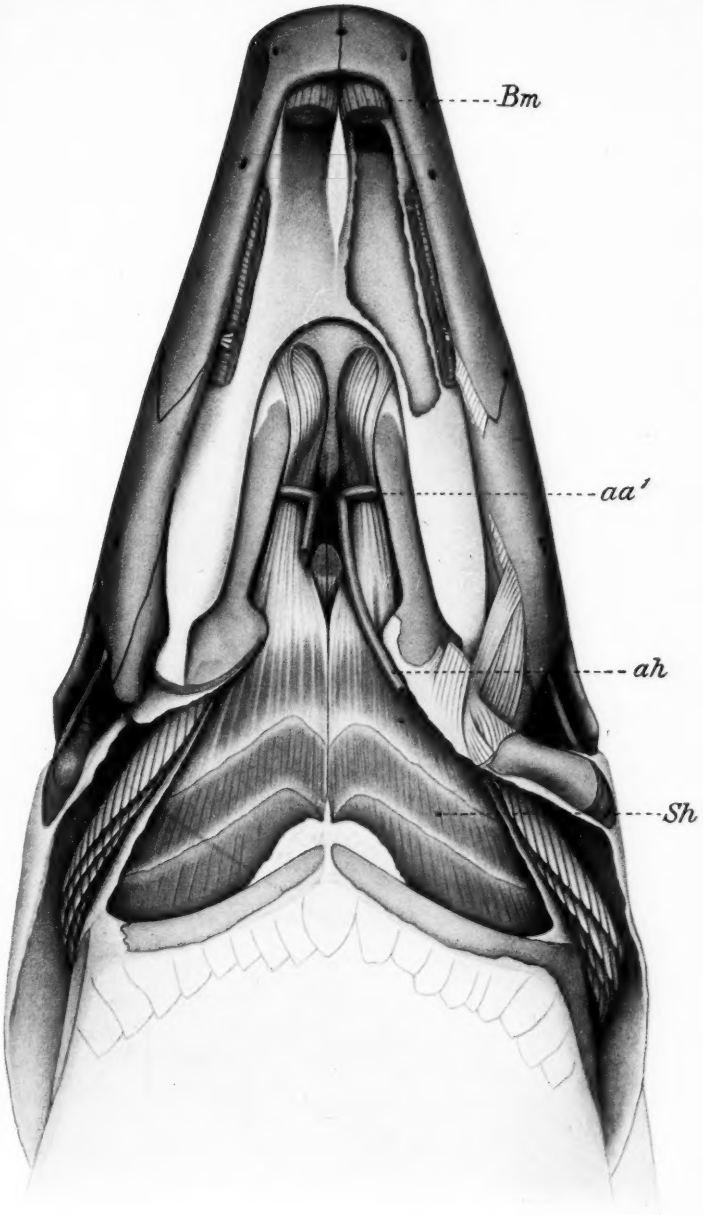


Fig. 52. A still deeper dissection of a second head of large *Polypterus bichir*. ×2.

UNIV. OF MICH.

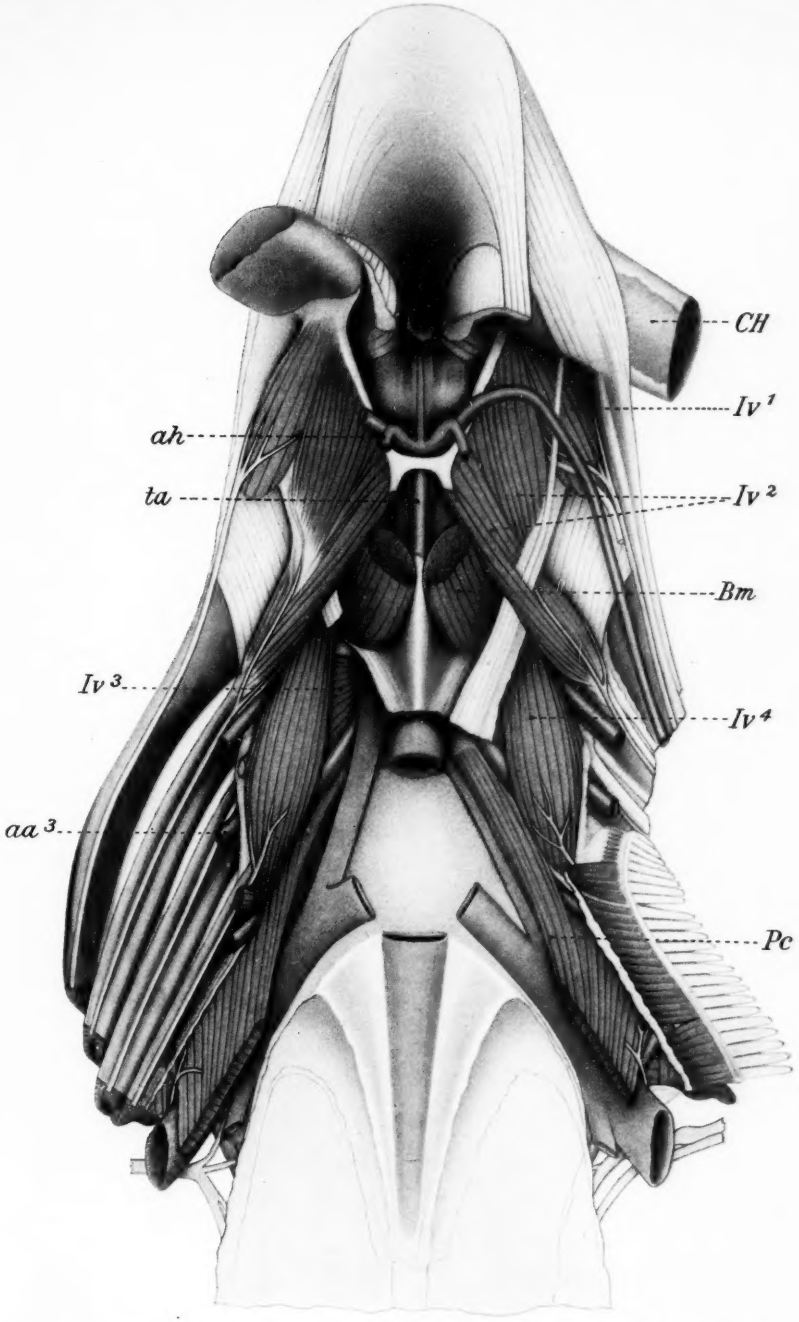


Fig. 53. Ventral view of the hyal and branchial arches of *Polypterus ornatipinnis*, with muscles attached. × 2.

UNIV. OF MICH.

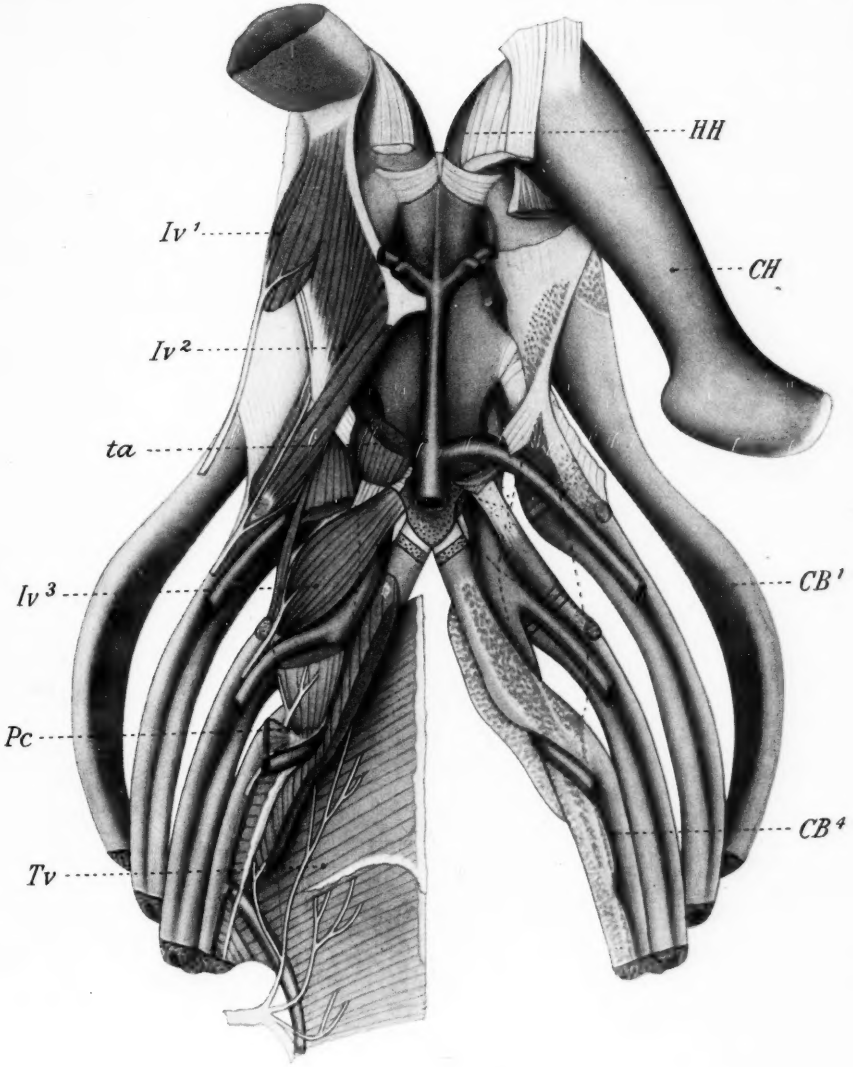


Fig. 54. A deeper dissection of the hyal and branchial arches of *Polypterus ornatipinnis*. × 2

UNIV. OF MICH.

ON THE HYPOTROCHANTERIC FOSSA AND ACCESSORY ADDUCTOR GROOVE OF THE PRIMATE FEMUR

By A. B. APPLETON.

Houzé, in 1883, drew attention to the occasional replacement in Man of the gluteal ridge by a fossa which he named the *fossa hypotrochanterica*.

It is the purpose of this paper to point out the presence of certain fossae in a similar position on other primate femora, which cannot be identified with the *fossa hypotrochanterica* of Man, since they are of a totally different nature.

In particular, a fossa is present on the femur of the Gorilla, Chimpanzee and Orang-outan, named in this paper the "**accessory adductor groove**[1]," which superficially resembles the *fossa hypotrochanterica* of Man. The homo-

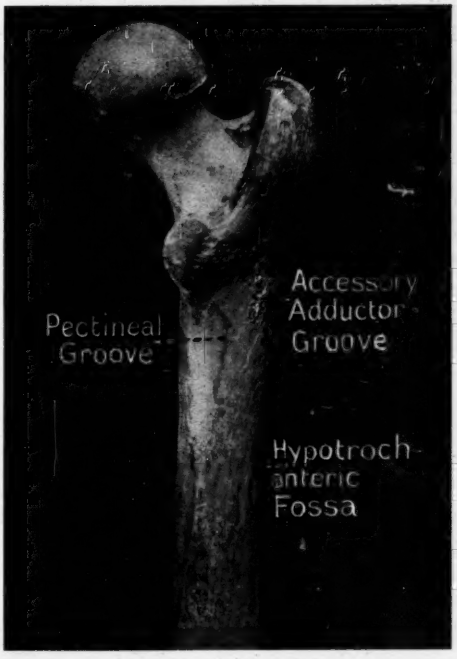


Fig. 1. Femur of Orang-outan (W.L.H.D). Posterior aspect of proximal end.

logue of the latter, however, is found in these apes in another situation, viz. on the outer aspect of the shaft well below the level of the lesser trochanter.

The resemblance between the *fossa hypotrochanterica* of Man and the accessory adductor groove of these apes is such that it may well be doubted

[1] *Vide* also fig. 2, showing a pair of such grooves in *Macacus nemestrinus*.

whether they would be distinguishable if we were not in a position to dissect the animals and demonstrate the muscular attachments. If all these femora belonged to fossil genera known to be closely related, one could hardly avoid the mistake of confusing the fossa and the groove.

Pearson and Bell, in their monograph on the femur (1), have confused the fossa and the groove in the Chimpanzee and Orang (p. 66, footnote 2).

The identity of the *fossa hypotrochanterica* is defined for us by Houzé as the site of insertion of *M. gluteus maximus* and in this sense later writers have dealt with it (von Török, Costa and Pearson).

The accessory adductor groove is the site of insertion of certain small muscle-slips belonging to the adductor musculature; these are supplied by small twigs from the obturator nerve. A detailed discussion of their morphology is reserved to another paper, but it is desirable to anticipate the conclusion that they are derived from the *MM. adductores longus, brevis* and *magnus*. They are accordingly named "accessory adductor muscles." They are apparently present in *all* Primates; and muscles which resemble them are found in other orders of mammals, e.g. *Carnivora* (*Canis*) and *Marsupialia* (*Perameles*).

The accessory adductor muscles (fig. 4) are situated between *M. obturator externus* on the one hand, and *MM. adductores longus, brevis* and *magnus* on the other hand, both at origin and insertion. The most caudad of the series is the homologue of the human *M. adductor minimus* and has a muscular insertion to the lateral lip of the accessory adductor groove. A common aponeurosis usually provides insertion for the remaining muscle-slips, of which there may be one (Man, Gorilla and Chimpanzee), two (Orang), or as many as four (*Cercopithecidae* and *Hapalidae*). This aponeurosis is attached to the floor of the accessory adductor groove; a reduplication of the groove sometimes occurs, corresponding to a reduplication of the aponeurosis (e.g. *Macacus nemestrinus*: II, W.L.H.D.).

In Man, the "upper belly" of *M. adductor brevis* is homologised as a part of the accessory adductor musculature of other *Primates*. It either shares insertion with *M. pectineus*, or it gains attachment somewhere between the pectineal line and *M. adductor minimus*. No accessory adductor groove is found at its insertion in Man.

ATTACHMENT OF *M. GLUTEUS MAXIMUS* TO FEMUR

Man: gluteal ridge, 3rd trochanter or *fossa hypotrochanterica*[1].

Gorilla, Chimpanzee and Orang-outan: a spiral fossa on the *lateral* aspect of the femoral shaft; this is the *fossa hypotrochanterica* of these animals[2]. It is the largest and most distally placed in the Gorilla.

[1] Pearson and Bell call attention to the frequency with which all types of Primogenial Man exhibit this fossa (1, p. 453).

[2] This is the fossa which Pearson and Bell named *fossa angulolateralis*, clearly distinguishing it from their "*fossa hypotrochanterica*" (accessory adductor groove); for they note "the presence of a ridge between" them in the Chimpanzee and Orang (1, p. 66, footnote 2).

Gibbon: gluteal ridge, opposite lesser trochanter.

Cercopithecidae: gluteal ridge, replaced or accompanied occasionally by a *fossa hypotrochanterica* (e.g. *Cercopithecus sab.* Juv. (Z.M.C. E 7788) and *Papio. ham.* Z.M.C.

The fossa takes the form of a groove in these two named specimens. A mere flattening is present in *Nasalis larv.* (A.D. 1 and R.C.S. 107), a slight groove in *Nas. larv.* Juv. (W.L.H.D. 1). It sometimes takes the form of a faint pit, with prominent medial lip. (*Semnopith. crist.* R.C.S., *Cynopithecus niger*, R.C.S. 175.)

A rough line forms a downward continuation of the gluteal ridge, or of the medial lip of the hypotrochanteric fossa when this is present.

Cebidae: two extreme types are found. On the one hand a very conspicuous gluteal ridge may be present, prolonged for some distance down the shaft; it is found in *Cebus* and *Mycetes*. On the other hand, there may be no projection at all (*Ateles*), but an extensive flattened area, of which the postero-medial margin is a little prominent; it extends considerably below the level of the lesser trochanter and recalls the spiral, laterally situated hypotrochanteric fossa of *Simiidae*.

Intermediate conditions between the two extreme kinds of gluteal attachment are found in *Brachyurus* and *Pithecia*. *Brachyteles* exhibits both a rough area pitted proximally, and a ridge on its medial side, both distal to the lesser trochanter.

Hapalidae: gluteal ridge is prominent.

Prosimiae: 3rd trochanter.

POSITION OF ACCESSORY ADDUCTOR GROOVE

Man: absent.

Gorilla, Chimpanzee and Orang-outan: about level with lesser trochanter, well to the lateral part of the posterior aspect. It is deepest and most proximally situated in the Chimpanzee.

Gibbon: small shallow groove (inconstant), midway between gluteal ridge and lesser trochanter.

Cercopithecidae: between gluteal ridge (or hypotrochanteric fossa) and lesser trochanter. Its proximal end is opposite the lesser trochanter, and it extends distally somewhat beyond the commencement of the pectineal groove. At least half of the pectineal groove is situated distally to the accessory adductor groove. These grooves approach one another as they proceed distally.

An *additional* accessory adductor groove is found in *Macacus nemestr.* and in *Semnopithecus*, marking the insertion of *M. adductor minimus*. It is situated slightly more distally than the customary accessory adductor groove, between it and the gluteal ridge. Dissection demonstrates the presence in both these species of an **aponeurosis** on the deep surface of *M. adductor minimus*, this

aponeurosis being attached to the additional groove[1]. The accessory adductor groove has the least proximal extent in *Papio*. It is situated closer to the hypotrochanteric fossa in *Papio* and *Cynopithecus* than in *Macacus*, *Semnopithecus*, *Cercopithecus* and *Nasalis*.

In one specimen of *Semnopithecus hosei* (W.L.H.D. 1) an "**accessory adductor ridge**" is present, replacing the customary groove. In a specimen of *Semnopithecus crist.* a short ridge is placed lateral to the groove (R.C.S. 100).

It is necessary to distinguish a faint depression which is frequently present at the insertion of *M. quadratus femoris* from an accessory adductor groove. It is immediately adjacent to the proximal end of the latter.

Cebidae: in many specimens no accessory adductor groove is present. One or more faint grooves are sometimes to be found in *Ateles*, *Cebus* and *Brachyteles*.

Hapalidae: a faint groove is placed close to the distal part of the gluteal ridge.

Prosimiae: absent (*vide infra*).

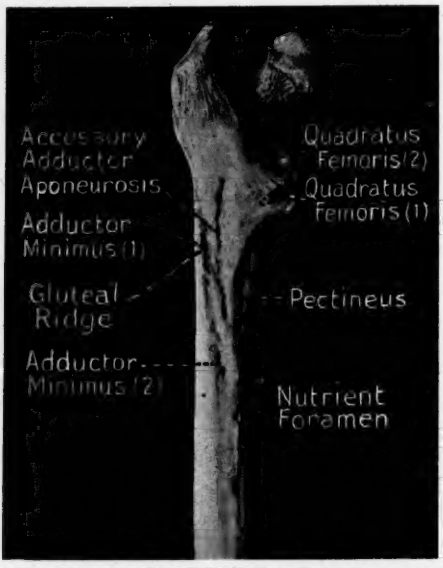


Fig. 2. Femur of *Macacus nemestrinus* (W.L.H.D.). Posterior aspect of proximal end.

Other grooves are present on the posterior aspect of the primate femur: besides the hypotrochanteric fossa and the accessory adductor groove (sometimes reduplicated). In most Primates a groove is present at the insertion of *M. pectineus*. The lateral lip is frequently raised and rough (especially in

[1] As a distinct condition it is to be noted that at the site of attachment of *M. adductor minimus* an apparent groove is sometimes formed between the prominent adjacent lips of hypotrochanteric fossa and accessory adductor groove (e.g. *Nasalis larvat.* Juv. W.L.H.D. 1; and *Cynopithecus niger*, R.C.S. 175) (cf. fig. 3).

certain *Cercopithecidae*) so that the attachment has more the character of a ridge than a groove. Of *Simiidae*, the Gorilla and *Hylobates* present the best marked grooves in the specimens examined: of *Cercopithecidae*, a *Colobus vell.* and a *Nasalis larv.* (Juv.) exhibit the most obvious grooves, while it is generally evident in *Platyrrhinae*.

The presence of this pectineal groove must be remembered in the identification of the accessory adductor groove. The distal ends of the two grooves approach one another, but the former is situated more distally, being always entirely *distal* the level of the lesser trochanter. Still another groove is frequently found marking the site of attachment of *M. vastus medialis*. It occurs sporadically throughout Primates, replacing (at the level of the pectineal line) the ridge to which *M. vastus medialis* is elsewhere attached. It is conspicuous in a femur of *Nasalis larvatus* Juv. (W.L.H.D. 1). It is mentioned only to distinguish it from the pectineal groove.

Dissection shows that the *MM. adductores longus* and *brevis* in *Cercopithecidae* are attached to a groove which occupies the middle one-third of the posterior aspect of the femur. It is called the "posterior fossa" by Pearson and Bell, and is present in most specimens both in their series and mine.

It is not continuous with either the hypotrochanteric fossa or the accessory adductor groove, and if attention is paid to the position of the foramen for the nutrient branch of *A. perforans prima* (where this is present) it will be found that the "posterior fossa" stops short of it. Now this artery always passes between the accessory adductor muscles on the one hand and *MM. adductores longus* and *brevis* on the other. It marks a distinct interval between two muscle masses, corresponding to which there are two separate grooves for their insertions on the femur.

One is the accessory adductor groove; for the more distal groove a more descriptive name would be the "**adductor groove.**" The adductor groove may be indeed duplicated (e.g. a *Cercopithecus sab.* Juv.), correspondingly with the sometimes independent aponeuroses of insertion of *MM. adductores longus* and *brevis*. Its lateral lip is in *Cercopithecidae* the more prominent, and to it is attached *M. adductor magnus*. It takes part in the maximum antero-posterior diameter of the femoral shaft, and its development must therefore be considered in a study of the pilastric index of these animals. The backward projection of this lip allows of such an attachment for *M. adductor magnus* as will minimise friction against the aponeurosis of the other two adductor muscles. A similar arrangement is seen in many *Artiodactyla* (e.g. *Cervus*) and most *Carnivora*.

Turning to Man and the Simiidae, this "posterior fossa" (or "adductor groove" as I prefer to call it) is said by Pearson and Bell to be absent. Evidently they have not recognised the downward displacement of the adductor insertions in the Gorilla, Chimpanzee and Orang. In all of these an adductor groove is a discernible feature distal to the "apex" of the popliteal space along

its medial side. The groove in them is rough, and tends in the Orang to become a ridge. In *Hylobates* the adductor groove is situated on the middle part of the shaft, as in *Cercopithecidae.* Man differs from all these in the possession of a projecting ridge on the middle one-third of the shaft, to which these two adductor muscles (as well as other muscles) are attached: this projection appears to have attained a maximum in Cromagnon man.

In *Platyrrhinae* a slight adductor groove is present. It occupies the middle part of the shaft, and is usually limited above and below by foramina for nutrient arteries to the femur.

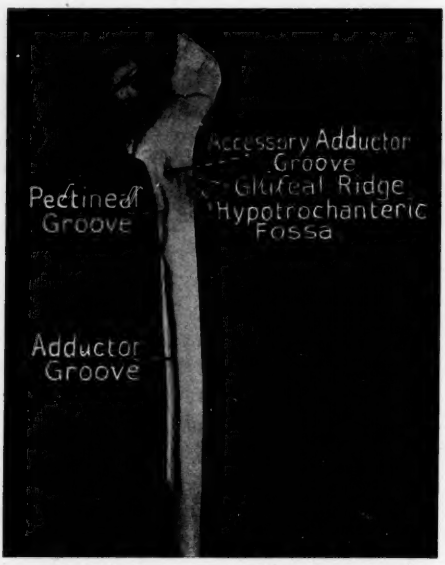


Fig. 3. Femur of young *Nasalis larvatus* (W.L.H.D.). Posterior aspect of proximal end.

POSITION OF ADDUCTOR GROOVE

Man: absent.

Gorilla, Chimpanzee and Orang-outan: shallow and rough: on proximal part of medial supracondylar line.

Gibbon: region of mid-shaft, between approximated septal lines of linea aspera.

Cercopithecidae: as in Gibbon, but longer and usually deeper (especially in *Nasalis* and *Semnopithecus*).

Platyrrhinae: similar to Gibbon.

Prosimiae: immediately below pectineal ridge.

Prosimiae present a great contrast to **Primates** in the disposition of muscular attachments on the posterior aspect of the femur.

They are indeed like the giant apes in the possession of *M. femorococcygeus*, attached along the lateral margin of the femur; and in the possession of a broad "interseptal" space on the femur between the attachments of the lateral and medial intermuscular septa (4). They differ (5), however, from most Primates in the presence of *M. caudofemoralis*[1], which is attached to a ridge (or rough area) at mid-shaft on the posterior aspect; and in the extensive insertion of *M. quadratus femoris* on the hollowed space between the lesser and 3rd trochanters. These two features constitute a most significant resemblance to *Insectivora* (e.g. *Tupaia*). *Prosimiae* are nevertheless distinguished from some *Insectivora* at least in the possession of an accessory adductor musculature. This is absent from *Tupaia*, and, so far as other *Insectivora* are concerned, Leche gives no hint of ever having seen it (6). Dobson (7, p. 81), however, detected its existence in Centetes and Solenodon, recording it under the name "adductor quartus."

A comparison of the femora of a Lemur and of a Primate is scarcely profitable without a special examination of the insertions of adductor and accessory adductor muscles. The accessory adductor muscles are attached in *Lemur* and *Tarsius* to the *medial* side of the shaft of the femur, below the lesser trochanter. They share attachment with *M. pectineus* to the pectineal ridge, and there is therefore no accessory adductor groove.

The pectineal ridge is, in *Lemur*, continued downwards for a short distance by a groove, to which *MM. adductores longus* and *brevis* are attached. This groove then is the adductor groove. It is homologous with the adductor groove on the middle third of the femur of *Cercopithecidae* and on the medial limit of the popliteal space of *Simiidae*. It is in *Prosimiae* placed above the mid-point of the shaft. In certain *Prosimiae* no adductor groove is present (*Tarsius* and *Galago*); in *Propithecus diad.* a tuberculated "**adductor ridge**" replaces it. In *Prosimiae* there is no *fossa hypotrochanterica*, for *M. gluteus maximus* is attached to the 3rd trochanter. The mode of attachment is not unlike that in *Hapalidae*.

The changes in site of attachment of muscles to the posterior aspect of the femur as we pass from *Insectivora*, through *Prosimiae* to the higher *Primates*, may be briefly indicated.

Along with enormous elongation of the femoral shaft as we pass from an Insectivore like *Tupaia* to *Prosimiae*, we find proximal shifting of the insertions of *MM. adductores longus* and *brevis*, and the differentiation of accessory adductor muscles which are attached still more proximally; they are all so far displaced that they are situated medially to the extensive attachment of *M. quadratus femoris* (fig. 5) instead of being medial to the insertion of *M. adductor magnus* (as in *Insectivora*, e.g. *Tupaia*). In passing from *Prosimiae* to *Primates* we note the disappearance of *M. caudofemoralis*, and of *M. femorococcygeus* (except in *Simiidae*). A reduction in the area of attachment of *M. quadratus femoris* is associated with considerable changes in the shape of

[1] This muscle is present in Hapalidae, at least.

the upper end of the femur and a lateral migration of the insertion of ***MM. adductores accessorii.*** This migration could hardly take place so long as ***M. quadratus femoris*** was attached to the whole of the space lateral to the pectineal groove (or ridge). The lateral situation of the attachment for accessory adductor muscles which is rendered possible by the restriction of ***M. quadratus femoris*** in ***Primates*** confers on those muscles a strong external rotatory action (*vide* fig. 4). The accessory adductor groove is thus found in ***Primates*** within the area formerly (in ***Prosimiae*** and ***Insectivora***) occupied by the insertion of ***M. quadratus femoris.***

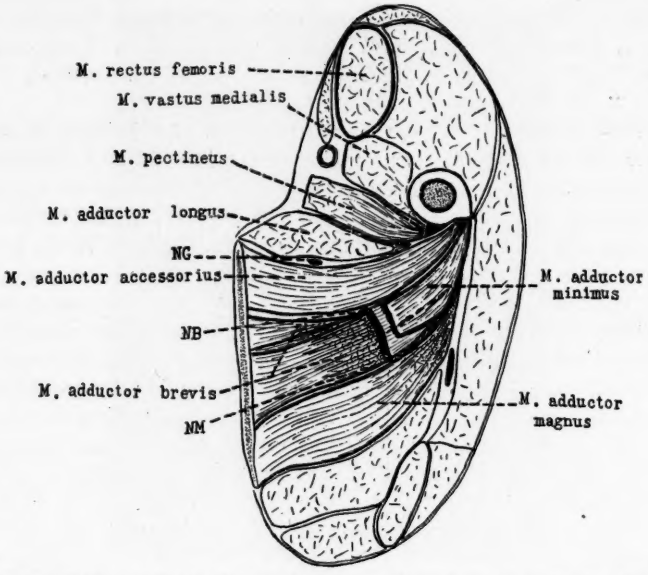


Fig. 4. Oblique Section of Thigh, *Macacus nemestrinus*, through pubic symphysis and accessory adductor groove. *NG* = Nerve to *M. gracilis*; *NB* = Nerve to *M. adductor brevis*. *NM* = Nerve to *M. adductor magnus*.

The retreat of ***M. quadratus femoris*** was associated also with an important change in ***M. adductor magnus.*** This muscle extended its femoral attachment proximally, and the proximal portion has, to a variable extent, become differentiated as ***M. adductor minimus.*** This, the most caudad accessory adductor muscle, is attached laterally to the accessory adductor groove. In certain ***Primates*** (e.g. ***Macacus nemestr.***) its deep (ventral) surface is aponeurotic near its insertion, and a second accessory adductor groove marks its site of attachment. In ***Primates*** the proximal displacement of ***MM. adductores longus*** and ***brevis,*** which occurs in ***Prosimiae*** is not reproduced. They are even attached *distally* to the middle of the shaft in the Gorilla, Chimpanzee and Orang. It is probable that proximal displacement in ***Prosimiae*** and distal

displacement in the *Simiidae* named is a function of the relative length of the femur (to pelvis). The more proximal attachment in the Gibbon supports this view (*vide* also Appleton 4, p. 385).

The position of *A. perforans prima* is worthy of attention, not only because it pursues a singularly constant course amid all the muscular changes. For the present study it is of special interest because it so frequently provides a nutrient branch to the femur, and the corresponding foramen is found also to exhibit some constancy in its position on the femur. It provides a land-

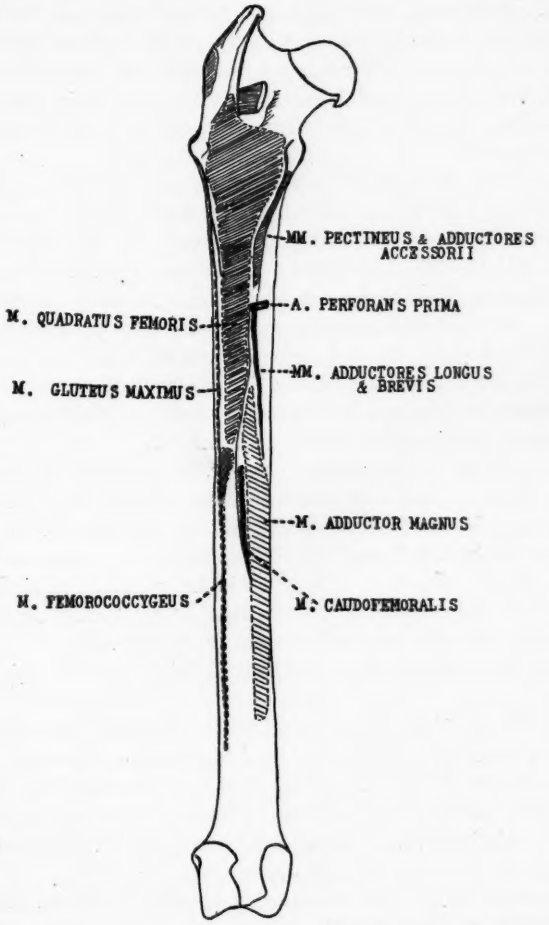


Fig. 5. Femur of *Lemur Catta*. Posterior aspect. Attention is directed to the large flattened area of insertion of *M. quadratus femoris*; the proximal limitation of *M. adductor magnus*; and the medially situated insertion of the *MM. adductores accessorii* on the pectineal ridge.

mark on the bone which exhibits far greater constancy than the muscular attachments around it. In *Tupaia* this artery runs proximally to the whole of the adductor musculature. In *Primates*, on the other hand, it passes through the interval between the adductor muscles proper, and the accessory adductor musculature. The appearance of the latter has in no wise disturbed the course of the artery across the bone. *Lemur* exhibits an interesting intermediate stage; for the most caudad of the accessory adductors is not yet differentiated. The artery, therefore, after passing[1] between the partially differentiated accessory adductors and *MM. adductores longus* and *brevis*, reaches the interval between *M. quadratus femoris* and *M. adductor magnus*. It then passes proximally to the whole *M. adductor magnus*. The *Primates* differ from this condition in the retreat of *M. quadratus femoris* to an intertrochanteric ridge, and the differentiation of a *M. adductor minimus* (from *M. adductor magnus*) with an insertion *proximal* to the *A. perforans prima*. *M. adductor minimus* has come between the artery and *M. quadratus femoris*.

The foramen for the nutrient branch of *A. perforans prima* is accordingly found in *Primates* when present[2] between the adductor groove and the accessory adductor groove. These grooves mark the site of attachment of distinctly differentiated muscle-groups, and this nutrient foramen is definitely related to the interval between them. The foramen is sometimes placed similarly in *Prosimiae*, but there is no accessory adductor groove proximal to it: instead of this Primate feature we find only a pectineal ridge and a hollowed or flattened space on which *M. quadratus femoris* is attached.

In this paper no attempt is made at discussing the significance of ridges and of fossae at the site of muscular attachments.

Facts established in this paper, however, suggest caution in the employment of the *fossa hypotrochanterica* for the natural classification of *Primates*. Pearson and Bell discuss the relationships among *Primates*, partly on the basis of the occurrence of this fossa, and of the alternative 3rd trochanter (1, pp. 83, 342, 483, 501). Apart from their failure to identify this fossa correctly in the large *Simiidae*, they apparently make the assumption that *Primates* exhibiting this fossa are to be considered mutually related forms: while a bony projection is to be regarded as a sign of affinity between animals (*op. cit.* p. 483).

Now the distribution of fossa and of the alternative gluteal ridge (when large, known as a 3rd trochanter) is an argument against this assumption. A classification based upon the presence of fossa or ridge is quite unlike the usually accepted natural classification of *Primates*. If we accept, as a particular case[3], the association of the genera *Ateles* and *Cebus*, in the same sub-family,

[1] In a *Galago* the foramen was situated medially to the pectineal ridge.

[2] When absent, a nutrient foramen is usually found just below mid-shaft. In *Ateles ater*, both nutrient foramina are sometimes present.

[3] Another such case is provided by the *Semnopithecinae*. In certain of these an accessory adductor ridge is a conspicuous feature, but in *Nasalis larv.* it is usual to find an obvious accessory adductor *groove*.

Cebinae (accepted by Pearson and Bell, *vide* Atlas, Table II), we must doubt the validity of their assumption. *Cebidae* as a whole indeed present great variety in the nature of the insertion of *M. gluteus maximus* to bone; but the two genera named, which belong to the *same* sub-family, present us with the two extreme conditions. In *Cebus* a very prominent ridge (properly described as a 3rd trochanter) is found: in *Ateles*, a rough hollowed, pitted or flattened area is found. Intermediate conditions of all stages are presented by *other* Cebidae. Among *Cercopithecidae* there is less variety; but here also we sometimes find a groove whereas in most of them a ridge occurs like that in *Cebus* (e.g. *Macacus*). *Hylobates* presents a distinct ridge: while the other *Simiidae* have a conspicuous fossa on the *lateral* aspect of the shaft which is more like the condition in *Ateles* than that of any nearer relatives.

Until more is known of a possible functional significance for the appearance of a fossa at the site of insertion of *M. gluteus maximus*, it must be precarious to argue[1] as to the nature of that insertion, whether fossa or ridge, in the common ancestor of *Hylobates*, the other *Simiidae* and Man.

The replacement of the pectineal groove by a ridge in certain individuals of certain species: the occurrence of a groove in some *Primates* at the origin of *M. vastus medialis*: the occurrence of an "accessory adductor ridge" in some *Semnopitheci* (conspicuous in *S. hosei* W.L.H.D. 1) instead of the more customary Primate groove: these facts are all suggestive of a problem akin to that of the occurrence of conspicuously "marked" bones in non-muscular human beings, and *vice-versa*. Individual variations in the production of bone-tissue at muscle-attachments seem to occur in Man: and it is uncertain at what point to describe the condition as pathological. We must reckon with the possibility of similar inter-special variations. The influence of age as a factor in the production of ridges at the sites of these fossae has not been investigated: it may be stated, however, that among the bones of *Cercopithecidae* examined, grooves mostly occurred in the immature bones, but were not confined to them.

In this paper attention is directed to the following points:

(1) The name *fossa hypotrochanterica* is conveniently reserved for a fossa, groove or pit at the site of insertion of *M. gluteus maximus* on the femur.

(2) In addition to this depression there occurs another groove on the posterior aspect of the Primate femur, in the neighbourhood of the lesser trochanter. It provides attachment for a specialised portion of the adductor musculature, and is given the name of "accessory adductor groove." With the specialisation of *two* accessory adductor aponeuroses in certain Catarrhinae, two corresponding grooves make their appearance on the femur.

(3) Grooves are also present in many *Primates* at the sites of attachment of *MM. pectineus, adductores longus* and *brevis*.

(4) All of the above-mentioned fossae and grooves may be replaced by ridges; the frequency of which varies in different species.

[1] See Pearson and Bell, 1, p. 483.

(5) The femur of *Prosimiae* is widely separated from that of *Primates* by differences of markings and muscular attachments. It presents a closer approach to that of *Insectivora.*

(6) Among *Primates* the hypotrochanteric fossa presents considerable variety of situation; an extreme condition is presented by the large *Simiidae.*

(7) With the reduction of the accessory adductor musculature in Man, there is an absence of any special groove or ridge for its attachment.

(8) In Man the hypotrochanteric fossa occupies a position approximating to that of the accessory adductor groove in other *Primates.*

My thanks are due to Prof. Wilson for valuable advice and criticism. Dr Duckworth generously placed many animals at my disposal for examination; and I am indebted to Sir A. Keith and Mr Forster Cooper for their kind permission to examine femora under their care.

Sources of specimens particularised in this paper:

Anatomy School, Cambridge ...	A.D.
Dr Duckworth, Private Collection ...	W.L.H.D.
Museum, Royal College of Surgeons	R.C.S.
Museum of Zoology, Cambridge ...	Z.M.C.

REFERENCES

(1) Pearson and Bell. *Drapers' Company Research Memoirs.* A Study of the Long Bones of the English Skeleton. Biometric Series, x. and xi. The Femur. 1919.
(2) Von Török, A. *Anat. Anz.* Jahr. i. S. 169–178. 1886.
(3) Houzé, E. *Bull. de la Soc. d'Anthr. de Brux.* Tom. i. pp. 21–54. 1883.
(4) Appleton, A. B. *Proc. Cambridge Philos. Soc.* vol. xx. pp. 374–387. 1921.
(5) —— *Proc. Cambridge Philos. Soc.* vol. xx. Gluteal Region of Tarsius Spectrum, pp. 466–474. 1921.
(6) Leche, K. *Svensk. Vet.-Akad. Handl.* 20 Bd. *The Pelvic Region of Insectivora,* pp. 374–387. 1883.
(7) Dobson, G. E. *Monograph of the Insectivora.* London, 1882.

A NEW INTERPRETATION OF THE BONES IN THE PALATE AND UPPER JAW OF FISHES

PART I

By H. LEIGHTON KESTEVEN, D.Sc., M.D., Chm.

Huxley's *Elements of Comparative Anatomy* bears the date 1864, and, with alterations in the form only of the terminology, his description of the bones of the fish palate and upper jaw as exemplified in the pike (*Esox lucius*) and the interpretations which his terminology implies have passed practically unchallenged to the present day. It is therefore only after long deliberation, under the impulse of a very real conviction, and with a full sense of the responsibility, that I now venture to question the whole of those interpretations, and offer an almost entirely new concept of the significance of the bones in the fish palate and upper jaw.

My reading leads me to recognise that I am not alone in feeling unconvinced by the old interpretations, and I am emboldened to advance my somewhat startling ideas, because I have reason to believe that the majority of investigators have based their descriptions of the structure and development of fish skulls on the assumption that the interpretations involved in their terminology were already sufficiently established, whereas this is not so. Huxley's defence of his interpretations is, in the light of our more intimate knowledge of structures and development, quite inadequate, and no serious defence of those interpretations has been advanced since. Especially have they not been analysed in the light of our knowledge of the development of the palate and chondrocranium not only of the fishes but of the vertebrata generally.

Throughout the following discussion the adult form and relations of the various bones are dealt with first, because the opinion is held that those factors in such problems as it is here attempted to solve are of primary importance. It appears to the writer that there is a tendency at the present time to abandon the cadaver and the scalpel entirely in favour of the wax plate model and the microtome, and that arising out of this tendency is another, that of allotting to adult form and structural inter-relationships less value than is their due. These tendencies are traceable directly to the reorientation of many of our ideas which resulted from the brilliant embryological studies of the latter end of last century and the early years of this. It was then demonstrated that adult form and position may disguise fundamental relationships which are obvious in the early stages of development. In each case, however, the demonstration has been that the fundamental condition has been truly retained, and being pointed out may always be recognised in the adult.

It is a truism that the boy is father to the man, and in our embryology we have recognised that he is often more nearly the son of his father than is the man he becomes. It were, however, well not to lose sight of the fact that the man is the direct descendant of the boy, and whatsoever the man hath, that must he have inherited from the boy.

Hence it is believed that, armed as we now are with the facts of embryology, and applying the knowledge of those facts all the time, it is permissible and, indeed, desirable to base our comparisons on the adult skulls first, and then, if need be, to test or modify them by an analysis of the ontogeny of the bones involved in the comparisons. The method has the added value that it lends itself to clarity of exposition—and brevity of discussion.

For a basis of comparison I have chosen as a typical teleostean palate that of *Promicrops*, a member of the Serranidae (one of the families of the Acanthopterygii), and in no way unique. It was selected primarily because, conforming in all essential respects to *Salmo*, *Scomber*, etc., it translated the vertical relations of the side bones of the palate and upper jaw arch, into horizontal relations, which permit of readier comparison with the palatal aspect of the skulls of tetrapods. *Promicrops* was preferred to *Platycephalus* and one or two other forms that were at my disposal, and in which the flattening towards one plane of the bones of palate and jaw is carried to a further degree, because the large size of the *Promicrops* skull made it exceedingly easy to disarticulate and determine with confidence the intimate relation of the various bones and their respective limits. Accordingly the following description of the upper jaw and palate has been carefully checked by the study of each bone separately, and by rearticulation of the disarticulated components.

THE UPPER JAW AND PALATE OF PROMICROPS
(Figs. 1 and 2.)

The premaxilla articulates with one bone only, the maxilla of its own side. Each is a tapering, slightly curved rod, presenting on the ventro-mesial aspect of the curve an attenuated isosceles triangular area closely set with strong sharp conical teeth. In the midline the bones unite one with the other by a fibro-cartilaginous union, and on either side of this symphysis send upward a pyramidal process. This solid pyramidal process is notched above, and its central portion stands up as a spur, which by the intermediary of a goodly thickness of cartilage and fibrous tissue comes to be connected to the upper surface of the mesethmoid and upper end of the anterior surface of the ethmo-vomer. The pyramidal process is that which in other forms has been designated the ascending process of the premaxilla. Its central portion may be termed the processus medialis, and the lower portion to the outer side of the notch the processus lateralis. Each medial process lies just medial to the medial border of the os nasalis, and is in the same plane therewith, being bound to it by fibrous tissue, and both lying immediately under the skin. The lateral

process, shorter and stouter than the medial, is overlapped at its upper and lateral border by the anterior flange of the premaxillary articular cup of the head of the maxilla. A low triangular lamina rises from the postero-mesial edge of the dorsal surface of the distal one-third of the premaxilla. This flange

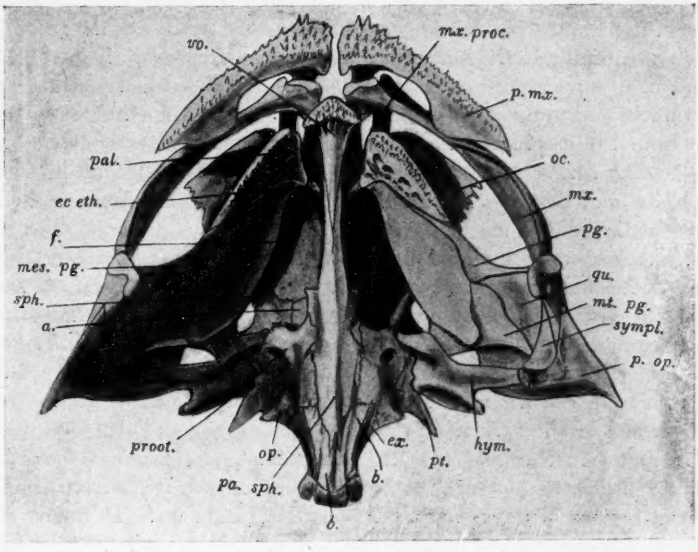


Fig. 1. *Promicrops itaiara*, palatal view of the complete skull.

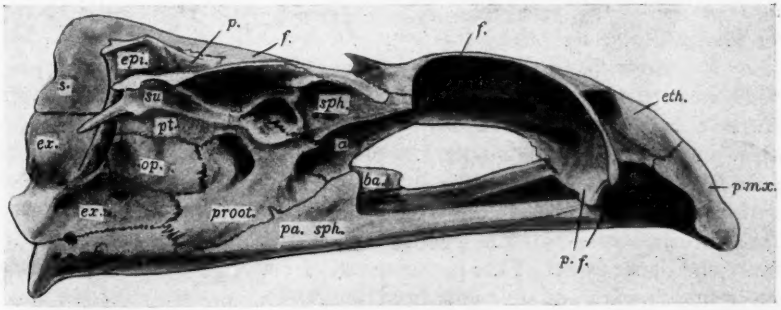


Fig. 2. *Promicrops itaiara*, side view of the cranium and bones derived from the chondrocranium.

rising abruptly from the bone at its own mesial limit tapers distally, and in its upper part lies behind the shaft of the maxilla.

The maxilla may be conveniently described as being composed of a head, a shaft and a distal spatulate portion. The swollen head of the bone lies for

the most part behind the base and lateral process of the ascending process of the premaxilla, being extensively hollowed out to articulate therewith. It may be that there is a small joint cavity behind the base of the ascending process, but certainly for the most part the space between the two bones is filled in with tough fibrous tissue, fibro-cartilage and hyaline cartilage. Particularly strongly developed is a curved rod of cartilage which is attached above in front to the posterior surface of the medial process of the premaxilla, below and laterally to the inner edge of the articulate cup of the maxilla, and behind in its upper portion to the ridge developed down the centre of the mesethmoid and upper part of the anterior surface of the ethmo-vomer.

It is well to emphasise the fact that the premaxillae articulate with the maxillae only, these latter with a process of the palatine found in no other vertebrate, and that for the rest these two jaw bones are hung to the skull by fibrous tissue only.

The vomer presents an enlarged body and a tapering laminate posterior process. The body is armed with teeth on the anterior portion of the oral surface, it articulates above with the mesethmoid and parethmoid. The posterior process lies beneath the anterior end of the parasphenoid. The upper portion of the anterior surface of the body of the vomer together with the anterior surfaces of the mesethmoid and parethmoids constitute the sloping posterior bony wall of the nasal organs.

The parasphenoid presents the usual shape and relations posteriorly. Anteriorly it becomes laterally compressed and extends far forward above the posterior process of the vomer to articulate not only with the hinder aspect of the ascending portion of the body of that bone, but also with the mesethmoid, and with the inner edges of the parethmoids. The articulations of the parasphenoid and the cranial components are shown in fig. 2, and call for no detailed description.

The palatine bone articulates with the parethmoid in two places, and bears two facets for these articulations. As viewed from the palatine aspect, the bone is triangular in outline. The shortest side of the triangle forms with the midline of the skull an angle a little less than a right angle. This angle is open anteriorly, and at its apex the palatine articulates with the palatine process of the parethmoid, the palatine facet being, of course, on the dorsal surface of the bone. Above this and slightly in front of it, there is a second facet of articulation with the parethmoid. This latter facet is born on the inner and upper aspect of the posterior end of a short, stout process, which, projecting forward and diverging from the midline, parallel with the short antero-medial edge of the bone, comes to overlie the head of the maxilla just lateral to the premaxillary articular cup. This process is that already referred to as providing the only bony attachment for the jaw bones. The palatine bone bears teeth along a narrow area close to the outer border of the bone. The postero-mesial border of the bone articulates with the mesopterygoid along the anterior one-third, and with the pterygoid for the rest of its length.

The pterygoid is a roughly boomerang-shaped bone, but with a short, comparatively broad spur standing out in a postero-mesial direction from near the centre of the convex edge. Behind the palatine the outer border is free. The inner edge articulates with the mesopterygoid as far back as the tip of the spur, and behind this with the quadrate. The blunt tip of the spur reaches the metapterygoid.

The general shape and articulations of the mesopterygoid, metapterygoid, quadrate, symplectic and hyomandibular are sufficiently clear in the drawing to need no description.

The mesethmoid, situated immediately above the ascending face of the vomer, suturates with the parethmoid on each side, and also forms a squamous suture with the antero-mesial edges of the frontals, the latter bone being the superficial element in the suture.

The irregularly shaped parethmoid besides its two articulations with the palatine, suturates with the vomer, the anterior end of the parasphenoid, the mesethmoid and the frontal, and articulates with the most anterior of the subocular bones. The sutures are all sutura notha, and the articulations, allowing of a very limited, but definite movement, were perhaps better termed amphiarthroses.

Having now figured and briefly described a typical teleostean palate, in accordance with general usage with the idea of providing a standard for comparison, the new interpretations of the components are stated briefly, and in the following pages are analysed in detail.

THESIS

(1) The maxillae and premaxillae of the majority of teleostean fish constitute an adventitious jaw, and are not homologous with the similarly named bones in other vertebrates.

(2) The labial cartilages well developed in most Elasmobranchs, present in one teleostome, and evanescent in amphibia, are structures homologous with the teleostean maxillae and premaxillae.

(3) The vomer of teleosts is homologous with the premaxillae of other vertebrates, it is certainly not the vomer of other vertebrates.

(4) The anterior portion of the parasphenoid of the teleosts is the homologue of the vomer of other vertebrates.

(5) The palatine of the teleostean skull is the homologue of the maxilla of other vertebrates.

(6) The mesopterygoid is the palatine.

(7) The pterygoid is the quadrato-jugal or jugal.

(8) The quadrate has been correctly homologised.

(9) The metapterygoid is the amphibian pterygoid.

(10) The parasphenoid corresponds to the vomer and pterygoids of the reptile.

(11) The parethmoid is the homologue of the reptilian prefrontal.

In fig. 3 the palate described above is reproduced in outline, bereft of the adventitious jaw. In this drawing the bones have been named in accord with my thesis. The figure is, as it were, a pictorial presentation of the thesis.

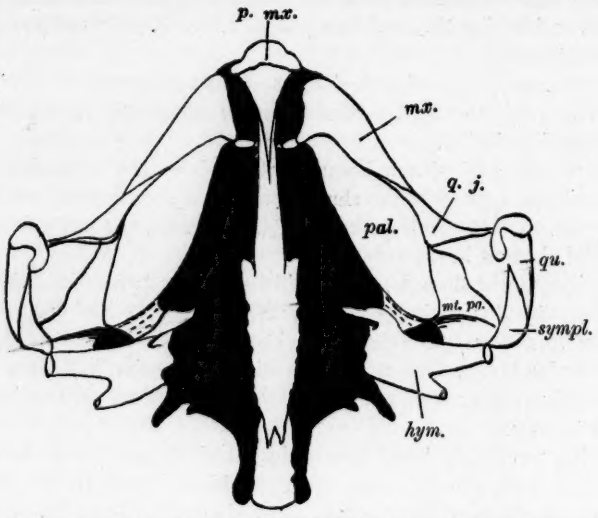


Fig. 3. *Promicrops itaiara*, outline of palate with adventitious jaw bones removed.

Fig. 4 is offered in support of the thesis, it is the same palate deprived of two of the suspensory bones, viz. the hyomandibular and the symplectic. Suspension is now depicted as being affected directly by the quadrate, which is drawn attached in the usual position to the side of the cranium. The metapterygoid has with the rest of the bones in the palate been approximated to the midline, and comes to underlie the parotic region. The palatine has been reduced in extent to create a subocular vacuity and to emphasise the position of the jugal and its relation to the maxilla and to the quadrate. The premaxilla has been provided with a median suture.

This drawing is, of course, hypothetical, but most of the innovations are present in some members of the bony fishes. Thus the approximation of the palatine to the midline is paralleled in *Platycephalus*. In *Lepidosteus* we find the upper jaw attached to the skull by the metapterygoid, and although a hyomandibular and a symplectic are present, it will be shown later that the attachment by the so-called metapterygoid approximates to the attachment shown in the hypothetical drawing. In *Amia* the vomer is paired, as also are premaxillae which are not homologous with the premaxillae of teleostei. In the muraenid eels maxillae and premaxillae are not developed.

Fig. 4, though, as stated, hypothetical, is not merely a figment of the imagination, and may fairly be compared on the one hand with fig. 3, and on the other with amphibian and reptilian palates. It resembles most nearly

the amphibian type, and when it is compared therewith one is struck by the absence of the prevomers, so well developed in the amphibian palate, and by the large size of the palatines.

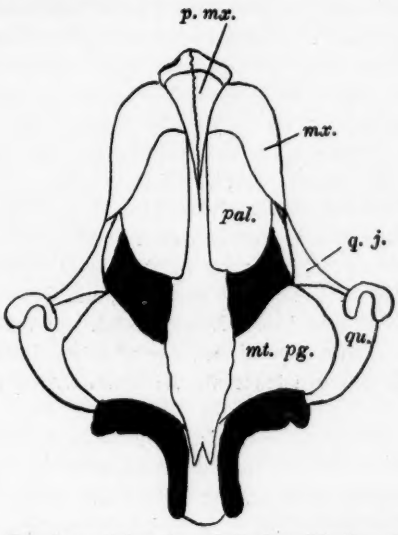


Fig. 4. *Promicrops itaiara*, hypothetical modification of fig. 3.

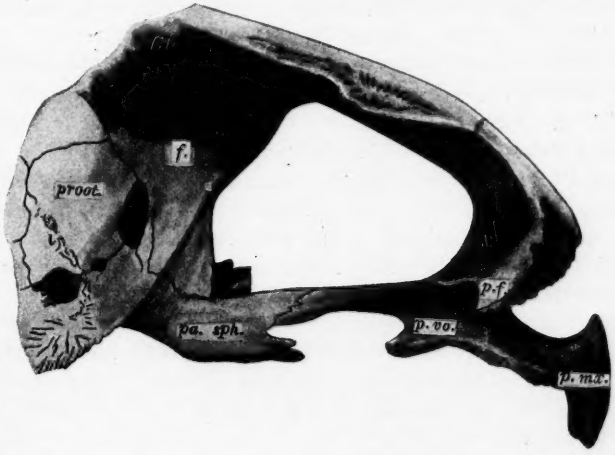


Fig. 5. *Chelonia midas* (*seu viridis*), median bones of facial skeleton from the side.

A comparison such as suggested serves to emphasise the fact that, granted the new interpretations are correct, the piscine palate falls into line with that of the rest of the vertebrata in all essential respects, with the exception of

the suspension by hyomandibular and symplectic. The essential fact which these new interpretations present is that the fish does not differ from other palates in the number of bones which enter into its composition.

The established interpretation of the piscine palate assumed the presence of two bones developed in relation to the subocular arch, whose origin and disappearance phylogenetically was quite inexplainable. They simply come and go in the bony fishes, and are not represented in any way whatever in any other vertebrates.

On the other hand, as soon as we recognise the two jaw bones as peculiar, adventitious jaws, their origin from the labial cartilages of the Elasmobranchs and Cyclostomes is at once comprehensible, and their disappearance may be studied in the various bony fishes and seen in their last stages in that class of vertebrates which probably next most nearly resembles their common ancestor, namely the Amphibians. Moreover, when we study the bones of the palate and attempt to trace them through the vertebrates, we do not now find ourselves with a superabundance of bones developed in relation to the subocular arch, but can trace all the bones through at least two other vertebrate classes.

This general defence of the thesis, admittedly, only stands if the bones, as now interpreted, conform in their adult relations and in their development to the similarly named bones in the rest of the vertebrata, but if in some respects that conformity be not as perfect between piscine and other palates as between those other palates *inter se*, then it is contended that the general considerations just advanced, must give confirmation to what might, in the absence of those considerations, be doubtful homologies.

In short, the general argument advanced is that the fishes, being descended from the same common ancestor as the other vertebrates, the palates of all are builded on a common plan.

Turning again to the established interpretation, we find labial cartilages present in Cyclostomes and Elasmobranchs, *absent* in bony fishes except Polypterus, present in Amphibia and absent in all other vertebrates. This then is a negative discontinuity in the serial homologies no less striking and incomprehensible than the positive discontinuity presented by the *presence* of the two extra pterygoid bones.

It is, moreover, a very emphatic coincidence that in *Polypterus* the only bony fish to retain a labial cartilage in the adult, Allis has argued that the maxillae and premaxillae are not homologous with the similarly named bones of other bony fish, but are homologous with the maxillae and premaxillae of other vertebrates.

THE INDIVIDUAL BONES

1. *Teleostean Maxilla and Premaxilla*

There is no doubt whatever that among the bony fishes the term maxilla has been applied to bones which are not homologous. In *Accipenser* (Parker,

1882) and in *Polyodon* (Bridge, 1878) a bone developed in relation to the subocular arch has been termed the maxilla. Inasmuch as there is no such relationship in the development of the so-called maxilla in the teleostean fishes the two bones cannot be homologous.

The contention that the teleostean maxillae and premaxillae are homologous with the labial cartilages in the elasmobranch fish is based on the relation of both structures to the fore part of the skull and to the lips. Both occupy labial folds which are in front of and lateral to the mouth border proper.

It is true that in teleostean embryos labial cartilages have been described (Parker, *Salmo.* 1873), but their relation to the development of maxillae and premaxillae has not, so far as I am aware, been determined. Their situation is, however, such that they may be generically related to the bones, and, moreover, in certain cases the developing jaw bones are found to have a lamina of cartilage on the posterior surface. In the Cyprinidae Sagemehl describes the development of a bony ossicle, the "os rostrale," in relation to this posterior covering of the premaxilla.

However, whatever be the genetic relation of the teleostean jaw bones to the embryonic labial cartilages, those cartilages are evancescent and in the adult their place is taken by the central ends of the jaw bones.

The similarity in situation of the labial cartilages is best illustrated in those elasmobranch fishes in which the two upper labial cartilages are best developed, and amongst these *Squatina* is a particularly useful example to quote, because the material for comparison is not difficult to obtain, and because there are excellent figures of the skull in Huxley's *Elements* and in Kingsley's *Comparative Anatomy of Vertebrata.* The two drawings are particularly fortunate in that they show not only the position of the cartilages with the jaw closed (Kingsley), but also the manner in which they are drawn down, exactly as do the premaxilla and maxilla, when the jaw is opened, owing to both being situated in the labial folds. It will be seen at once that in *Squatina* if the cartilages were carried forward, or if the snout were a little shorter, the situation of the cartilages would be exactly that of the two jaw bones in the teleostean fishes.

If, in the following pages, it is demonstrated that the piscine vomer and palatine bones are homologous with the maxillae and premaxillae of the tetrapods, that becomes at once an added reason for regarding the piscine maxillae and premaxillae as the homologues of elasmobranch labial cartilages.

2. *The Teleostean and Tetrapod Vomer and Premaxillae*

The premaxillae of the tetrapods present the following features of form and position. Occupying the front segment of the upper jaw they suturate one with the other medially and each with the maxilla laterally. They develop a palatine process which contributes to the formation of the antero-median portion of the bony palate and floor of the nasal organ, this process may or may not suturate with the vomer above, it generally suturates with the

prevomers when they are present. In front the premaxillae may (Lacertilia, Ophidia, Aves and Amphibia) or may not (Chelonia, Crocodilia and Mammalia) send a process upward between the anterior nares, anterior nasal process (processus praenasalis, Gaupp), or they may bound the nostril laterally by an ascending posterior nasal process (processus extranasalis, Gaupp). The processus praenasalis suturates with the nasal bones which lie to either side of them. The processus extranasalis is separated from its fellow by the anterior nares, and above it is wedged in between the nasal bone to its inner side and the ascending facial process of the maxilla.

The so-called premaxilla of the teleosts presents one single bony contact, that with the maxilla. This contact is in no sense a suture, but is an amphiarthrosis in which, it may even be, an actual joint cavity is present. This articulation is not situated like the suture in the tetrapods at the lateral edge, but is between the back of the pyramidal process of the premaxilla, and a glenoid cavity on the front of the body of the maxilla, so that the latter bone intervenes between the premaxilla and the rest of the skull.

It may be thought that the medial process of the premaxilla is directly comparable with the tetrapod processus praenasalis. The processus medialis is united by firm fibrous and cartilaginous tissue to its fellow and the two are similarly bound to the central ridge of the mesethmoid, they lie in the same plane as the nasal bones, and in their upper portion lie between the divergent anterior ends of these bones, there is, however, no suture formed, and the interval, which may be quite marked, is filled in by loose connective tissue.

In the tetrapods the nasal bones are situated above the nares and at times extend forward to form their outer border in its upper portion. In the bony fish the nasal bones lie between and, where they are juxtaposed to the processus medialis, are for the most part anterior to the nares.

The processus praenasalis of the tetrapods is by its inner margin in contact with the cartilaginous septum nasi, and in the fish the cartilage which binds the two medial processes to the median ridge of the mesethmoid might be regarded as the homologue of the nasal septum. This, however, is not so, for though it lies between the two nasal sacs it is a secondary fibro-cartilaginous inter-osseous union and is no part of the primary chondrocranium. The structures are analogous but not homologous.

The resemblance between the processus medialis and the processus praenasalis is then purely topographical and not one of true similitude.

The teleostean premaxilla possesses no suture with neighbouring bones, it is separated from the rest of the craniovisceral skeleton by the maxilla and there is no relation to the palatine or vomer. In all these features it differs fundamentally from the tetrapod premaxilla.

It is proposed to compare the teleostean vomer with the tetrapod premaxilla, it will, therefore, be convenient to institute that comparison before dealing with the development of the bones, and then discuss all three together.

Broom has, I believe, satisfactorily established the identity of the mam-

malian vomer with the reptilian parasphenoid, and I have advanced reasons for regarding the latter as a derivative of the anterior end only, of the amphibian parasphenoid. If these contentions, or if Broom's alone be accepted, the vomerine nature of the teleostean "vomer" is at once disproven. Wilson's masterly analysis of the relations of the prevomer, dumbell bone, in *Ornithorhynchus* (Wilson, 1894) and Broom's own description of the prevomers in *Miniopterus*, would seem to have so sufficiently established the duality of prevomers and vomers and the parasphenoid origin of the true vomer, that it is with surprise that one reads Kingsley's statement that "more evidence is needed on these points" (Kingsley, *l.c.*). However, in view of that statement it would appear advisable to assume for the moment that the application of the name vomer to the teleostean bone signifies homology with the bones that in recent years we have learned to term prevomers. In the reptilia these bones are developed in relation to the inner side and under surface of the paraseptal cartilage. When as in the Chelonians the attachment of the paraseptal cartilage to the lower edge of the septum nasi takes place early and rapidly becomes extensive, the prevomers are developed in relation to the sides of the lower edge of the septum. In the Amphibians there is no paraseptal cartilage, and the floor of the nasal capsule is very early completed, the lower edge of the septum nasi being quite early expanded laterally. Under these conditions the prevomers develop on the under surface of the nasal floor medial to the widely separated nares.

In all these forms the bone is situated under the nasal floor, which in the midline anteriorly is similarly supported by the palatine plates of the premaxillae. In no case does the prevomer extend forward to the anterior limit of the nasal floor.

On the other hand the piscine vomer is situated beneath the most anterior portion of the ethmoid cartilage, which is the homologue in the fish of the nasal floor in the tetrapod. In some cases, Acanthopterygii, actually ossifying the whole of that portion of the cartilage.

There can be little doubt that the piscine vomer is a more anterior element than the tetrapod prevomer and the two structures are not homologous.

In the arrangement of an argument such as the present, wherein each section, being proven, lends support to the contention of the next, there is a tendency to rely upon that support. I am anxious not to fall into such a fallacious method of argument, for though I believe that the reasons advanced are sufficient to justify the view adopted, I am fully aware that the nature of the problem attacked does not admit of absolute proof of the verity of that view, and that the last appeal will always be to the personal equation.

Let us then for the moment *assume* either that the above contention constitutes proof that the piscine jaw bones together form an adventitious jaw not present in the tetrapods, or that no such bones are present in piscine skull, and then examine the situation of the vomer. (See figs. 2 and 3.)

Situated in the centre of the gap in front, it develops a strong median

palatine process. Its upper surface forms the floor of the anterior portion of the nasal organ. Its antero-ventral margin is tooth bearing. It is flanked by, and at times suturates with (*Esox*, *Platycephalus*, *Sebastodes*) a bone having a palatine lamina, a tooth-bearing border and at times a facial process (*Esox*). In these relations the vomer resembles the tetrapod premaxilla. There is another feature wherein the resemblance is marked. The anterior end of the parasphenoid laterally compressed, vomerine in situation and form, suturates with the upper surface of the palatine plate of the vomer in the midline, and, as already stated, we have strong reasons for believing that anterior portion of the parasphenoid to be the true tetrapod vomer.

The vomer possesses no ascending facial process and there is therefore no suture or articulation with the nasals.

Turning next to the development of these three bones. The teleostean premaxillae are developed as paired ossifications from a membranous stroma, perhaps in relation to the embryonic labial cartilages, quite independently of the chondrocranium, in front of the ethmonasal cartilage.

The teleostean vomer is developed as a single ossification, in membrane as an ectochondral bone to the anterior portion of the ethmonasal cartilage, or endochondrally replacing that cartilage in its anterior portion.

The tetrapod premaxilla is developed in membrane in relation to the front and anterior portion of the floor of the cartilaginous nasal capsule.

Now, of course, if the two bones in front are true premaxillae then the vomer cannot be, but we have seen that they may be quite reasonably regarded as constituting an adventitious jaw derived from the labial cartilages. The relation, situation, and development of the vomer all resemble those of the tetrapod premaxilla, with the single exception of the absence of the premaxilla-nasal suture. It is reasonable to regard the bones as homologous. The vomer is certainly not the vomer of tetrapods and if it be not the tetrapod premaxillae, *then it would appear to be a bone present in the bony fishes and unrepresented in all other vertebrates.*

3. *The Teleostean Maxilla and Palatine, and the Maxilla of the Tetrapods*

In the tetrapods the maxillae present the following features. Situated on either side of the premaxillae they constitute the greater part of the gape. They suturate with the premaxillae in front and with the jugal behind. Its extensive palatine lamina suturates with that of premaxilla, with the palatine bone and commonly with the prevomers. A well developed ascending facial process forms more or less of the side wall of the nasal organ, and suturates with the processus extranasalis of the premaxilla, the nasal bone, and with the frontal or prefrontal. Above the jugal and below the frontal suture the maxilla commonly articulates with the lachrymal. Mesial to the lachrymal, there may be union with the ethmoid. There is a maxillo-vomerine suture along the inter-maxillary suture for more or less of the length of the palatine plates, when these meet in the midline and a true vomer is present. Though

in man and the apes the maxilla participates in the boundary of the orbit, this is unusual in Mammalia, but the rule in the rest of the tetrapods.

The teleostean maxilla does not suturate with any bone. By amphiarthrosis as we have already seen it articulates with the back of the pyramidal process of the premaxilla and by fibrous and cartilaginous tissue it is loosely but firmly bound to the vomer and mesethmoid. Also by amphiarthrosis it articulates with the maxillary process of the palatine. This latter articulation is in no way similar to the sutural connection between palatine laminae of the maxillae and palatine bones in the tetrapods.

Comparing these two brief descriptions it is apparent that there are no features of similitude in their relations. True, both bear teeth and both may be said to be situated in the gape. I would contend that the teleostean bone is morphologically outside the gape.

The palatine bone of the teleosts articulates with the parethmoid of its side by two fibro-cartilaginous amphiarthroses, and by amphiarthrosis or suture with the lateral edge of the vomer. The root of the maxillary process forms an incomplete, low side wall for the nasal cavity. It will be shown later that there are very real reasons for regarding the parethmoid as the homologue of the prefrontal of the reptiles[1]. Though there is no articulation of the palatine with the frontal or nasal, there is yet in its situation and relation to other elements sufficient evidence to justify the statement that it is more probably homologous with the tetrapod maxilla than is the so-called teleostean maxilla. Especially is this so if it be admitted that the so-called vomer is in truth a premaxilla.

This statement appears to receive further support from the development of the three bones.

The teleostean maxilla is developed, as has already been stated, quite independently of and not in juxtaposition with the chondrocranium.

The teleostean palatine is the most anterior of the bones developed in relation to the outer side and under surface of the palatine portion of the subocular arch, is, in fact, developed around the place of attachment of that arch to the lateral expanse of the ethmoid.

The tetrapod maxilla is developed in relation to lateral plates of the ethmonasal cartilage, and to the anterior attachment of the subocular arch, when that is present.

The teleostean palatine and tetrapod maxilla in their developmental history present much greater similitude than do the latter bone and the teleostean maxilla.

In view of all the facts it is reasonable to regard the teleostean palatine and the tetrapod maxilla as homologous bones.

[1] This is not a new idea. Sagemehl is quoted by Allis (1898) as applying the name prefrontal to the parethmoid in Amia. Allis himself adopts the name in the explanation of his figures in the Scomber paper, 1903.

4. *The Teleostean Mesopterygoid and the Palatine of the Tetrapods*

If the homologies arrived at in the last section hold good, then it becomes necessary to seek in the fish palate for the homologue of the tetrapod palatine. A similar statement might be made at the beginning of each section of the analysis of the topography and development of the individual bones, but would make the whole argument hinge on section 1. For that reason this form of argument is not stressed in any other section, though believed to be good.

The tetrapod palatine is found in the palate, suturating with the palatine plates of the maxilla, between and behind which they are placed. There is a median inter-palatine suture. There is commonly sutural connection with the prevomer in front. The vomer when present as a separate entity suturates with both palatines along the dorsal aspect of the inter-palatine suture.

The palatine may suturate with the vomerine anterior end of the parasphenoid, or with the anterior end of the pterygoids. There is commonly a suture along the posterior border of the bone with the os transversum, when that bone is present.

Now, it will be found that, unless the conclusions of the previous and subsequent sections of this analysis be accepted as presenting the correct interpretations and homologies of the bones in the fish palate, then the adult mesopterygoid does not possess one single relation to surrounding bones in common with the palatine of the tetrapods. This, however, is the only homology argued which is dependent in the adult condition on the acceptance of the other sections. Even here, moreover, the new idea is supported by the development of the two bones.

The palatine bone of the amphibians is developed in relation to the ventral and medial surface of the anterior end of the subocular arch, extending thence across the under side of the posterior region of the expanded nasal floor.

The mesopterygoid of the fish is developed in relation to the same portion of the subocular arch, there being no expansive nasal floor, that relation does not occur, and the bone extends medially and backward to contribute largely to the formation of the bony palate, and in this *situation* it resembles strongly the palatine of the reptiles.

5. *The Teleostean Metapterygoid, the Amphibian Pterygoid and the Reptilians Os Transversum*

I have in an unpublished paper argued the homology of these bones and need not again canvass the subject. It is sufficient to state here that the arguments then adduced in favour of the homologies were and are quite independent of anything advanced in the present contribution. It is intended here to regard those homologies as already established.

6. *The Teleostean Pterygoid and the Quadrato-Jugal of the Tetrapods*

The pterygoid bone in the fishes suturates with the quadrate, with the metapterygoid, the mesopterygoid and the palatine. In the tetrapods the quadrato-jugal is sutured to the quadrate behind and to the maxilla or jugal in front, and at times just reaches the hinder end of the palatine. Both bones are developed ectochondrally in relation to the subocular arch immediately in front of the quadrate. (Compare especially the development in the amphibian skull.)

The situation of the two bones is essentially the same, such differences as are present are directly due to the expansive development of the other two pterygoid bones, which, meeting one another and the pterygoid, fill in the area where, in the tetrapods, we find the suborbital vacuity. If one imagine an amphibian in which, to the condition present in the *Ichthyophis*, there were added the broad posterior portion of the pterygoid present in *Branchiosaurus*, then would the quadrato-jugal be in contact along its length with the quadrate, the pterygoid, the palatine and the maxilla. That is to say with the quadrate behind, the maxilla in front, and the other two bones developed in relation to the subocular arch between these two. On the other hand, if we imagine the reverse process applied to the fish palate, and devise a subocular vacuity, then we have a quadrat-jugal suturing with the quadrate behind and with the two bones developed in relation to the inner and outer aspect of the point of attachment of the subocular arch to the ethmo-nasal cartilage.

If, finally, we add to these arguments those advanced in the previous sections, then the weight of probability lies with the contention that the piscine pterygoid is the homologue of the tetrapod quadrato-jugal.

7. *The Teleostean Parethmoid, the Reptilian Prefrontal and the Mammalian Lacrymal*

As previously indicated the name prefrontal has already been applied to the parethmoid by more than one writer. Thus Swinnerton (1902, p. 531) says: "In the higher vertebrates the squamosal, post frontal and *prefrontal* are purely dermal bones, but the bones in the teleostean skull to which these names are frequently applied, viz. pterotic, sphenotic and *parethmoid*, are cartilage bones with a possible dermal origin." I am not aware of any extended defence of the homology assumed by the procedure, and therefore believe that an analysis of their development and relations is desirable. The nomenclature has not found acceptance in the text books. Kingsley gives it qualified acceptance. In the text the bone is referred to as the ectethmoid, and in the explanation of the drawing of Scomber skull he follows Allis and terms it the prefrontal.

In the adult skull (fig. 2) the piscine parethmoid is sutured to the vomer, the mesethmoid, the frontal and the front of the parasphenoid. The vomer

is below it in front, the mesethmoid is to its inner side and in advance of it, the frontal is above and behind it, whilst the parasphenoid suturates with its lower medial edge. Its situation relative to the orbit behind and the nasal organ in front is, as in the case of the reptilian, prefrontal. It forms the anterior perpendicular wall and anterior moiety of the roof of the orbit and the posterior wall of the cavum nasi. The superior naso-tectal process which in the reptiles forms the posterior portion of the roof of the cavum nasi is, however, not developed to protect the teleostean nasal capsule, and there is no articulation with the nasal bone medially above the organ. The olfactory nerve reaches the olfactory sac by passing forward through a sulcus on the inner margin of the bone, or it perforates the inter-orbito-nasal plate of the bone near its inner margin. Sensory branches of the fifth and seventh nerves pass forward to the snout through a foramen or a sulcus on the inner margin of the same plate above the olfactory nerve. Below, the parethmoid presents two facets for the articulation of the palatine, and one for the anterior periocular scute, (subocular bone).

In most of these features the resemblance to the reptilian prefrontal is very striking, especially is this so if it be kept in mind that a greater or lesser degree of dissimilarity must result from the increasing size and complexity of the nasal organ.

In the reptiles the prefrontal is sutured to the frontal above, and with the ascending, facial, process of the maxilla below. It may suturate with the nasal in front of the frontal. The lower margins of the inter-orbito-nasal plates suturate with the palatines.

The olfactory nerve enters the sac by passing forward against the upper end of the inner margin of the inter-orbito-nasal plate. The sensory fibres of V and VII also pass that margin as they enter the bony nasal capsule, on their way to the front of the snout.

The large reptilian nasal capsules have, as it were, been excavated out of solid sub-, retro-, and inter-nasal ethmoidal cartilage, which in the fish either remains as such encased in mesethmoid, parethmoid, and vomer, or is replaced by these as massive bones. The mesethmoid bone has gone, and is represented by the hinder portion of the cartilaginous nasal septum, later to reappear in the mammals as the perpendicular plate of the ethmoid.

If in the fish skull the mesial portion only of the mesethmoid were present, there would be no contact of that bone with the two parethmoids, and an inter-parethmoidal vacuity would result, absolutely comparable with the inter-prefrontal vacuity in the hinder wall of the cavum nasi of the reptiles.

If, further, in the fish skull the expanding nasal organs should excavate the ethmoid cartilage right down to the dorsal surface of the bony palate, and at the same time develop large anterior nares at that level, the portion of the vomer which articulates with the parethmoid would be abolished.

Under these circumstances the piscine parethmoids would suturate with the frontals above and with the parasphenoid below.

The suture with the vomerine anterior end of the parasphenoids reproduced in the crocodilian skull, where the conjoint pterygoids retain the archaic parasphenoid features and the prefrontal bones articulate with the vomerine portion of the bone (Kesteven, 1919).

As against so many features of similarity, the fact stated by Swinnerton (*l.c.*) that the parethmoid is a cartilage bone with a possible dermal origin, whilst the reptilian prefrontal is a purely dermal bone, cannot be conceded the greater weight. From several investigators, more especially Sewertzoff, Sagemehl and Gaupp, we have learned that more than one of the cartilage bones is phylogenetically of dermal origin.

It is to be concluded then that the piscine parethmoid and the reptilian prefrontal are in all probability homologous bones.

Fig. 5 is offered for comparison with fig. 2.

In view of the facts and observations advanced by Gaupp it would appear that the bone which palaeo-osteologists have designated prefrontal in the Cynodonts would be more correctly termed preorbital, and that the prefrontal is really that which has been designated lacrymal. I would endorse Gaupp's conclusion that the reptilian prefrontal is the homologue of the mammalian lacrymal, and accept his term "adlacrymal" for the variable "lacrymal" of the reptilian skull.

It was intended to offer some observations on several of the more aberrant piscine palates, but material which I had hoped for has failed to reach me, and this matter is therefore reserved for a future contribution, when I shall have had an opportunity of dissecting heads of *Amia*, *Lepidosteus*, Accipenserids, and perhaps, if one of my confreres reading this will assist me, also *Protopterus*.

BULLAH-DELAH,
NEW SOUTH WALES.
January 1921.

BIBLIOGRAPHY

ALLIS (1897). "The cranial muscles and cranial and first spinal nerves in *Amia calva*." *Jour. Morph.* vol. XII. No. 3, p. 487.

—— (1898). "The morphology of certain bones of the cheek and snout of *Amia calva*." *Jour. of Morph.* vol. XIV. No. 3, p. 425.

—— (1903). "The skull and the cranial and first spinal nerves and muscles in *Scomber scomber*." *Jour. of Morph.* vol. XVIII. Nos. 1 and 2, p. 45.

BRIDGE (1879). *Phil. Trans. Roy. Soc.* (On *Polyodon*), vol. CLXIX. p. 683.

BROOM (1896). "On the Homology of the Palatine Process of the Mammalian Premaxillary." *Proc. Linn. Soc. N.S.W.* vol. X. p. 477.

—— (1902). "On the Mammalian and Reptilian vomerine bones." *Proc. Linn. Soc. N.S.W.* vol. XXVII. p. 545.

GAUPP, E. (1905). "Neue Deutungen auf dem Gebiete der Lehre vom Saugetierschädels." *Anat. Anz.* Bd. XXVII. p. 273.

KESTEVEN, H. L. (1916). "The relations of the Amphibian Parasphenoids." *Jour. of Anatomy and Physiology*, vol. L. p. 303.

KESTEVEN, H. L. (1919). "The pterygoids in Amphibia and Reptiles and the parasphenoids." *Jour. of Anat.* vol. LIII. p. 223.

KINGSLEY, J. S. (1919?). *Comparative Anatomy of the Vertebrates.* (2nd edition). London. Undated.

PARKER, W. K. (1873). "On the structure and development of the skull in the Salmon." *Phil. Trans. Roy. Soc.* vol. CLXIII. p. 95.

—— (1882). "On the structure and development of the skull in the Sturgeon." *Phil. Trans. Roy. Soc.* vol. CLXXIII. p. 139.

SAGEMEHL (1891). "Das Cranium der Cyprinoiden." *Morph. Jahrb.* Bd. XVII. Hft. 4, p. 489.

SWINNERTON, H. H. (1902). "A contribution to the morphology of the teleostean head skeleton." *Quart. Jour. Micr. Sci.* vol. XLV. p. 503.

WILSON, J. T. (1894). "Observations on the anatomy and relations of the dumb-bell bone in Ornithorhynchus." *Proc. Linn. Soc. N.S.W.* vol. IX. p. 129.

ABBREVIATIONS

a. alisphenoid; *b.* basi-occipital; *ba.* basi-sphenoid; *ec.eth.* ect-ethmoid; *epi.* epi-otic; *eth.* mesethmoid; *ex.* ex-occipital; *f.* frontal; *hym.* hyomandibular; *mes.pg.* mesopterygoid; *mt.pg.* metapterygoid; *mx.* maxilla; *mx.proc.* maxillary strut of the palatine; *oc.* anterior periocular; *op.* opisthotic; *p.* parietal; *p.f.* prefrontal; *p.mx.* premaxilla; *p.op.* preopercular; *p.vo* prevomer; *pa.sph.* parasphenoid; *pal.* palatine; *pg.* pterygoid; *proot.* prootic; *pt.* pterotic; *q.j.* quadrato-jugal; *qu.* quadrate; *s.* supraoccipital; *sph.* sphenotic; *su.* sulcus hyomandibularis (for attachment of the hyomandibular bone); *sym.* symplectic; *vo.* vomer.

ON TRUNCATED UMBILICAL ARTERIES IN SOME INDIAN MAMMALS

By BASANTA KUMAR DAS, M.Sc. (Allahabad),
Zoological Department, Muir Central College, Allahabad, U.P., India.

In Volume liv of this *Journal*[1] Dr W. N. F. Woodland described and figured, as an unique anatomical fact, the blindly-ending umbilical arteries of the common Indian goat. As he remarked, it is difficult or impossible to call to mind "any other instances in Vertebrates of arteries ending blindly in this fashion." In February of this year I was engaged in examining a very abnormal female puppy (pariah dog) and I noticed that the umbilical arteries also ended blindly in this type. Dr Woodland then suggested to me that it might be worth while to examine systematically as many Indian mammals as I could obtain to ascertain if these truncated umbilical arteries are the rule in India. Acting on this suggestion I have examined 28 species of Indian mammals, and in 26 of these truncated umbilical arteries were found to exist.

Roughly speaking, these truncated umbilical arteries can be separated into two groups: (1) those which are of approximately uniform diameter from their origin to their extremity, and (2) those which diminish in diameter to some extent towards their extremity.

THE YOUNG DOMESTIC PIG (*SUS CRISTATUS*, DOMESTICATED) AN EXAMPLE OF A MAMMAL POSSESSING TRUNCATED UMBILICAL ARTERIES OF UNIFORM DIAMETER.

Each truncated umbilical artery (text-fig. 1, *TUA*) in the very young domestic pig (one ♂ specimen, about four days old, examined) arises, as usual, as the external division of the two branches into which the dorsal aorta bifurcates at its posterior limit. The diameter of these arteries, near the point of their origin, is approximately three times that of the internal iliac arteries (*INTIL*)—a superiority in size which is apparently found in all *young* mammals and in them only: in all adult mammals the internal iliacs are either equal in calibre to the umbilical arteries or larger. These truncated umbilical arteries, invested by the peritoneal folds, become, after a short course, slightly dilated (here giving off the small arteries—*UMA*—to the uterus masculinus) and then, reverting to their original diameter (which is maintained throughout their length), run straight backwards to the bladder (*B'*), to the wall of which they are loosely attached. Vesical arteries (*VESA*), two on each side, are given off from the upper half and on the inner side of each umbilical artery.

[1] Part 4, p. 309, 1920.

OTHER EXAMPLES OF TRUNCATED UMBILICAL ARTERIES OF UNIFORM DIAMETER

Bos bubalus and *Bos indicus*.

The only particular in which the truncated umbilical arteries of the buffalo, *Bos bubalus* (half a dozen specimens examined, three ♂ and three ♀), and the bullock, *Bos indicus* (half a dozen specimens examined, three ♂ and three ♀) differ from those of the young pig is that the arteries, instead of running straight backwards, have, unlike those of the pig, a slightly sinuous course and do not come into contact with the bladder, as shown in text-fig. 2. Curiously enough, in these species, three to four very fine vesical arteries (text-fig. 2, *S*) are given off from the very extremity of the umbilical arteries and run close together in the peritoneal folds on their way to the bladder. The equal calibres of the internal iliacs and umbilical arteries are clearly shown.

Boselaphus tragocamelus.

There is one interesting feature to be noted in the nilgai or blue bull, *Boselaphus tragocamelus* (two specimens examined, both ♂). The vesical arteries (text-fig. 3, *VESA*), five to ten in number, soon after their origin from the truncated umbilical arteries, anastomose to a slight extent, as represented. The truncated umbilical arteries are slightly narrower in external diameter than the internal iliacs, and the left one (*LTUA*) in an abnormal male specimen was nearly twice the length of the right one (*RTUA*), but in normal individuals both the truncated arteries are equal in length (the normal condition is shown on the left-hand side of the figure, *RTUA*), and do not come into contact with the anterior part of the bladder, as is also the case in the bullock and the buffalo. In the abnormal umbilical artery (*LTUA*) the truncated end was continued on as a tag-like muscular process (*M*) in which ran two small arteries (*G* and *H*), given off from the hinder end of the left truncated artery. I did not ascertain the connections of the muscular process or the contained arteries. A couple of very fine twigs (*D* and *E*) was given off from one (*H*) of these small arteries to supply the posterior wall of the left truncated artery, as shown.

Felis torquata (domesticated).

The truncated umbilical arteries of the bazaar cat, the domesticated *Felis torquata* (four specimens examined), are very similar to those of the young pig, the only point of difference being that the truncated vessels (of the same diameter as the internal iliacs) do not pursue a straight course, but curve round (over a fatty mass lying in contact with the urinogenital organs) in the manner shown in text-fig. 4. Six vesical arteries are given off from their lower extremities. I might also add that under certain abnormal conditions both the truncated umbilical arteries, as well as the internal iliacs, may be given off from a single main vessel arising either from the right division of

the dorsal aorta (as found in an abnormal ♂ specimen) or from the left division (as found in an abnormal ♀ specimen).

Felis pardus.

In the panther, *Felis pardus* (two ♂ specimens examined), the truncated umbilical arteries (smaller in calibre than the internal iliacs) run almost straight down to the bladder, the blind extremity of each artery being slightly dilated, and from the inner side of each dilated end a fine vesical artery (text-fig. 5, *T*), in addition to a main vesical artery (*VESA*) coming off from its upper half, is given off to the bladder.

Platanista gangetica.

The truncated umbilical arteries of the Gangetic dolphin, *Platanista gangetica* (one ♀ specimen examined), are of the same diameter as the internal iliacs at their origin, run towards the bladder in a slightly curved course (as observed in a preserved specimen and represented in text-fig. 7) and are intimately connected with the anterior end of the bladder, differing in this last respect, from the arteries of the pig, the cat and the panther. Two vesical arteries (*VESA*), as well as from one to four uterine arteries (*UTA*), are given off from the truncated umbilicals. Other noteworthy facts are that there are no external iliac arteries (due to the absence of the posterior limbs) and that the caudal (*CA*), as well as the internal iliac arteries (*INTIL*), soon after their origin, break up into the well-known arterial "retia mirabilia" (*PA*), the caudal plexus being continued into the wide haemal canal.

Canis familiaris (Pariah dog).

The truncated umbilical arteries in the adult pariah dog pursue a straight course for the greater part of their length, but are much convoluted towards their extremity, in which region they are also intimately connected with the bladder wall. It is important to note that in the pariah dog puppy the umbilical arteries are at least equal in diameter to the internal iliac arteries, but that in the adult they are distinctly smaller. The same fact is seen in the pig as already stated, and has also been observed in the young porcupine.

Another important feature to note concerning the umbilical arteries of the Indian dog is that in both the puppy (three examples) and the adult (two examples) the blind terminal portions have the lumen largely filled with hard greenish translucent granular matter—like sand in consistency. In the puppy the granular matter occupied about the last fifth of the blind artery; in the adult the granule-occupied region was relatively smaller. This granular matter was non-crystalline and was found to be insoluble in chloroform, alcohol, glacial acetic acid and even in aqua regia, though the last caused the granules to disintegrate and to evolve a small quantity of gas (CO_2?). The origin and nature of this refractory granular matter are at present undetermined, but the deposit must be a result of the separation-out from

the blood of the blood pigments—a process which, occurring as it does in the living animal, is in itself of considerable physiological interest. It remains to be mentioned that the wall of the portion of the artery containing the granular matter was deeply tinged with brown colouring matter, and that I have found no other instances of this granular matter in the umbilical arteries of other Indian mammals.

Macacus rhesus.

I have figured (text-fig. 6) the condition of the umbilical arteries in the common brown monkey, as an example of a primate.

Camelus dromedarius.

In the single-humped camel, *Camelus dromedarius* (one ♂ specimen examined), the truncated umbilical arteries appear to be similar to those described for the young domestic pig, save that, in the specimen examined (which I think was abnormal), the right truncated umbilical artery and the right internal iliac artery take their origin separately from the posterior end of the dorsal aorta. Both the truncated arteries are, as usual, smaller in calibre than the internal iliacs and do not reach the bladder, although the posterior end of the left truncated artery was continued on as a muscular process (as in the abnormal nilgai already described above) which was attached to the wall of the bladder.

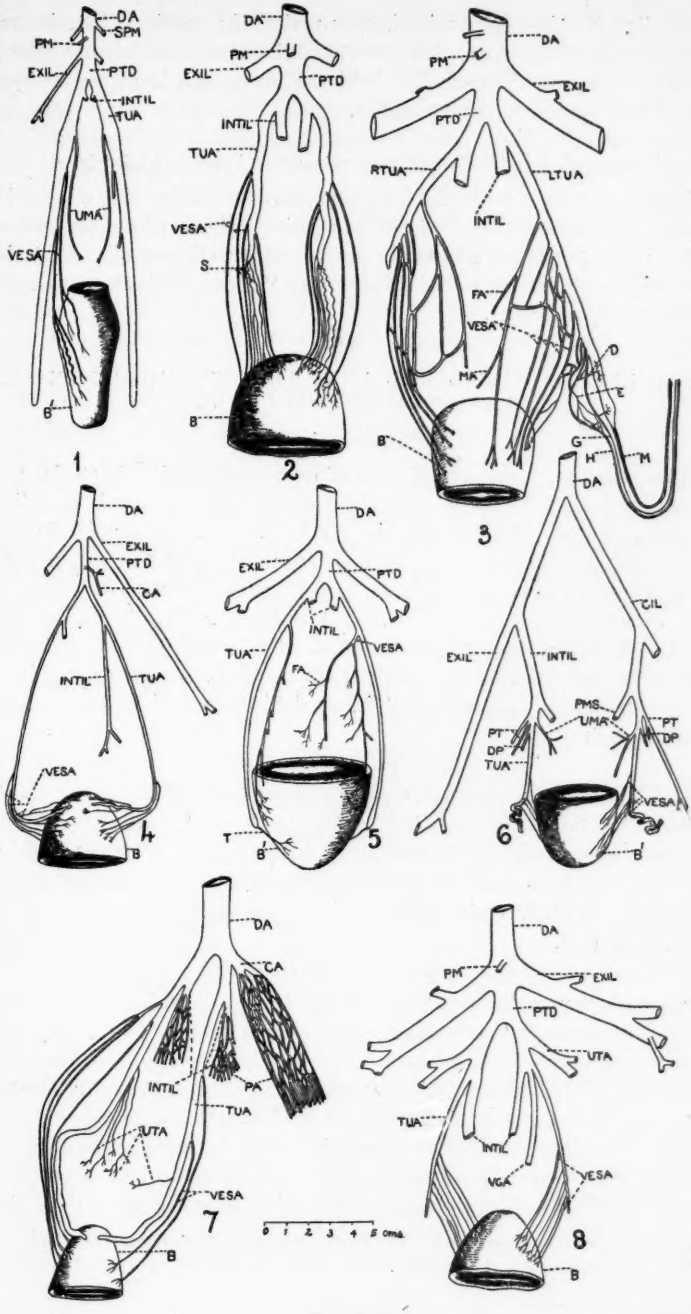
Pteropus medius and *Vespertilio muricola.*

It is interesting to note that in two of the common representatives of the Indian cheiroptera, e.g. the Indian fruit-bat or "flying-fox," *Pteropus medius* (five specimens examined, all females) and the mustachioed bat, *Vespertilio*

DESCRIPTION OF FIGS. 1—8

Fig. 1 (× 2): ventral aspect of the truncated umbilical arteries of uniform diameter in the young domestic pig, *Sus cristatus*, domesticated; fig. 2 (× 1): the same in the bullock, *Bos bubalus*; fig. 3 (× 1): the same in the abnormal male nilgai or blue bull, *Boselaphus tragocamelus*; fig. 4 (× 3): the same in the bazaar cat, *Felis torquata*, domesticated; fig. 5 (× 1): the same in the panther, *Felis pardus*; fig. 6 (× 2): the same in the brown monkey, *Macacus rhesus*; fig. 7 (× 3): the same in the Gangetic dolphin, *Platanista gangetica* (in this figure the umbilicals are represented as having been pulled to the left of the median line); fig. 8 (× 1): ventral aspect of the truncated umbilical arteries (with diminishing calibre) in the doe of *Antilope cervicapra* ("black buck").

B, bladder (contracted); *B'*, contracted bladder turned backwards; *CA*, caudal artery; *CIL*, common iliac artery; *D*, small artery given off from the vessel *H*; *EXIL*, external iliac artery; *FA*, small artery to the fat body; *G* and *H*, small arteries running along the muscular process; *INTIL*, internal iliac artery; *LTUA*, left truncated umbilical artery; *M*, muscular process attached to the posterior extremity of the left truncated umbilical artery; *MA*, small artery to the mesentery; *PA*, arterial plexus of the caudal and the internal iliac arteries; *PM*, posterior mesenteric artery; *PMS*, artery supplying the muscles of the pelvic cavity; *PT*, artery supplying the proximal region of the thigh; *PTD*, posterior trunk of the dorsal aorta; *RTUA*, right truncated umbilical artery; *S*, small vesical arteries from the posterior extremities of the truncated umbilical arteries; *SPM*, spermatic artery; *T*, small vesical artery given off from the dilated extremity; *TUA*, truncated umbilical artery; *UMA*, artery to the uterus masculinus; *UTA*, uterine artery; *VESA*, vesical artery; *VGA*, vaginal artery. The centimetre scale indicates the amount of reduction in size that has occurred in reproducing the figures.


DA
SPM
PM
EXIL
PTD
INTIL
TUA
UMA
VESA
B
1
DA
PM
U
EXIL
PTD
INTIL
TUA
VESA
S
B
2
DA
PM
EXIL
PTD
RTUA
LTUA
INTIL
FA
VESA
MA
D
E
G
H
M
B
3
DA
EXIL
PTD
CA
INTIL
TUA
VESA
B
4
DA
EXIL
PTD
INTIL
TUA
VESA
FA
T
B
5
DA
CIL
EXIL
INTIL
PMS
UMA
PT
DP
PT
DP
TUA
VESA
B
6
DA
CA
INTIL
PA
TUA
UTA
VESA
B
7
0 1 2 3 4 5 cms
DA
PM
EXIL
PTD
UTA
TUA
INTIL
VGA
VESA
B
8

Figs. 1—8

muricola (two specimens examined, both males) the umbilical arteries are of the usual truncated type[1]. They are slightly smaller in calibre than the internal iliacs and do not reach the bladder. The vesical arteries are apparently given off from their hinder extremities.

Equus caballus (India), *Equus asinus* (India) and *Ovis vignei.*

The only other types which I have examined and which are to be included among those possessing the truncated umbilical arteries of uniform diameter are the Indian horse, ass and sheep, and the truncated umbilical arteries in these types require no special description, the vesical arteries not arising from the extreme tip of artery.

TRUNCATED UMBILICAL ARTERIES WHICH DIMINISH IN DIAMETER DISTALLY

Antilope cervicapra.

As an example of the second type of truncated umbilical arteries it may be mentioned that in the doe of *Antilope cervicapra* ("black buck"—one specimen examined) the two arteries (text-fig. 8, *TUA*), smaller in calibre than the internal iliacs, gradually taper from the point of origin towards their posterior extremities which are loosely connected with the wall of the bladder. These truncated arteries have terminally a slightly sinuous course and give off six to seven vesical arteries. It is a curious fact that the left internal iliac artery (near the origin of the common vaginal artery) is much narrower in calibre than the right internal iliac (on which side there is no vaginal artery).

Semnopithecus entellus.

In the langúr or hanúmán monkey, *Semnopithecus entellus* (one ♀ specimen examined) the truncated umbilical arteries, instead of gradually diminishing in calibre, become slightly dilated at about two-thirds of the distance from their origin and then suddenly become very narrow (and convoluted) before terminating. A single vesical artery arises from each umbilical in the latter third of its length.

Some common local rodents.

In some common local rodents (except the common Indian rat) such as the hare, *Lepus ruficaudatus* (four specimens examined, two ♂ and two ♀), the palm-squirrel, *Sciurus palmarum* (two specimens examined, both ♂) and the porcupine, *Hystrix leucura* (four specimens examined, one adult ♂, two young ♂ and one young ♀) the truncated umbilical arteries (smaller in diameter, as usual, than the internal iliac arteries in the adult) have gradually tapering extremities which are so intimately associated with the wall of the bladder that (save in the hare) they are not easily visible with the naked eye. Strange

[1] In most cases the truncated umbilical arteries in these cheiroptera are wholly or only partially covered with black pigment cells.

to say, in the common Indian rat, ***Mus rattus*** (six out of eight specimens examined, one adult and two young ♂, and three adult and two young ♀) the truncated umbilical artery was present on the ***right*** side only, there being ***no truncated artery on the left side.*** This remarkable truncated umbilical artery of the right side (slightly smaller in calibre than the right internal iliac artery) was a thread-like structure white in colour save for its posterior extremity, which was tinged with deep brown pigment. On the left side, however, a small vesical artery was given off from the left internal iliac artery, which evidently capillarised over the wall of the bladder, the latter being also supplied by several minute vesical arteries, as usual, given off from the truncated umbilical artery. Lastly, I must state that in two rats (one ♂ and one ♀) I was unable to detect any truncated umbilical artery on either side.

Other types.

In addition to the preceding mammals possessing tapering truncated umbilical arteries the following may be mentioned without special description: the Indian wild boar, ***Sus cristatus***[1] (one adult ♂ specimen examined), the jackal, ***Canis aureus*** (two specimens examined, one adult ♂ and one young ♂), the Indian fox, ***Vulpes bengalensis*** (one ♀ specimen examined), the Indian palm-civet, ***Paradoxurus niger*** (two specimens examined, one adult ♂ and one young ♀) and the common Indian mongoose, ***Herpestes mungo*** (two specimens examined, one ♂ and one ♀).

TWO INDIAN MAMMALS NOT IN POSSESSION OF TRUNCATED UMBILICALS

Pteromys inornatus.

In one badly preserved male specimen of a less common rodent, viz. the large red flying-squirrel, ***Pteromys inornatus***, from the Simla Hills, I could detect no truncated umbilical arteries, though such may exist.

Crocidura caerulea.

In the common Indian insectivore, the grey musk shrew or musk-rat, *Crocidura caerulea* (four specimens examined, two ♂ and two ♀), I was unable to detect any truncated umbilical artery, but small vesical arteries were given off from one of the branches of the internal division of the common iliac artery.

FEATURES IN THE HISTOLOGY OF THE TRUNCATED UMBILICAL ARTERY

(1) The lumen of the truncated umbilical artery is much smaller relative to that of such a normal artery as the internal iliac: e.g. in the jackal the diameter of the umbilical artery at its anterior end is only 1/31 of that of

[1] Probably the adult domesticated pig has also tapering truncated umbilical arteries, so differing from the young individual.

the internal iliac, in the porcupine 1/25, civet cat 1/13, pariah dog 1/10, "black buck" 1/6, langúr monkey $\frac{1}{4}$, mongoose 1/3, panther and *Macacus rhesus* 1/25 and the bullock $\frac{1}{2}$.

(2) As a general rule the walls of the umbilical arteries are thicker (absolutely) than those of the internal iliac arteries (from 1·2 to 3·5 times as thick); only in the porcupine, *Hystrix leucure*, were the walls of the two arteries of the same thickness. The thickening in some cases occurs in the middle coat (*tunica media*) of the artery (jackal, camel, panther, civet cat); in others in the outer coat (*tunica adventitia*) of the artery ("black buck," nilgai, horse, ass, bullock, wild boar, cat); in others both coats thicken (macacus, langúr monkey and dog). In the porcupine the walls of the umbilical artery are not thicker than those of the internal iliac. All these statements are founded on accurate measurements of transverse sections of the arteries.

(3) Posteriorly the lumen of the truncated umbilical artery gradually narrows and becomes broken up into small intercommunicating spaces which finally terminate towards the tip, the centre of the artery being occupied with a core of muscle.

CONCLUSION

The presence of these truncated thickened umbilical arteries in such a large number of Indian mammals is of considerable interest to the student of embryology and possibly of physiology. It is possible that this feature is correlated with existence in a tropical climate, but we cannot assume this until it is known whether mammals in other tropical countries possess similar umbilical arteries. It is difficult to suppose that these persistent embryonic structures perform any function in connection with the bladder, though it would be pleasing to imagine that they had something to do with the conservation of the water of the urine. It is probable that these umbilical arteries are merely conspicuous embryonic vestiges and have no particular function, and this view is supported by the facts that in young mammals they are very much larger, relative to the internal iliacs, than those found in adults, the lumen in the adult umbilical artery being very reduced in size.

In conclusion I wish to express my great indebtedness to Dr W. N. F. Woodland for his kind criticisms and advice, and the keen interest he has taken in my work. My best thanks are also due to him for assistance in writing up this paper.

EARLY DEVELOPMENT AND PLACENTATION IN *ARVICOLA* (*MICROTUS*) *AMPHIBIUS*, WITH SPECIAL REFERENCE TO THE ORIGIN OF PLACENTAL GIANT CELLS

By G. S. SANSOM, B.Sc.

Honorary Research Assistant, Department of Anatomy, University College, London.

INTRODUCTION

This work was begun in 1913 at the suggestion of Professor J. P. Hill, partly on material belonging to him and partly on that collected by myself. At that time we had no early stages in our possession and it was not until the Spring of 1919 that I was able to obtain a sufficiently complete series.

The water voles, in the wild state, were killed during the months of March and April when their first breeding season occurs. The ovaries and uteri were, in every case, removed immediately after death and placed in fixing fluids. Of the latter, the following gave the most satisfactory results:

(i) Bouin's picro-formol acetic.

(ii) Alcohol sublimate-acetic mixture, consisting of 60 parts absolute alcohol, saturated with $HgCl_2$, 30 parts chloroform, 10 parts glacial acetic acid.

One of the finer cytological fixatives would have been most valuable but, owing to the nature of development in these rodents, the embryo is shut off from the uterine lumen by a considerable thickness of compact tissue and a fixing agent of great penetrative power was essential.

The ovaries and uteri were cut in serial sections, some at 8μ some at 10μ. Where, as in later stages, a complete series was not necessary, some sections were cut at 5μ thickness.

Throughout the work I am very greatly indebted to Professor J. P. Hill for much kind assistance, advice and encouragement.

I am also indebted to Mr F. J. Pittock of University College for advice on photographic matters connected with my preparation of the photomicrographs.

The early development and placentation of *Microtus amphibius* does not appear to have been worked out hitherto, but with the material now available it is possible to form a clear view of the general course of events.

In the allied species of voles, *Arvicola agrestis* and *Arvicola arvalis*, a certain amount of work has already been published, but my own observations are not in complete agreement with those of Disse as regards the uterine changes and origin of the giant cells, which latter form such a conspicuous feature in the placentae of these rodents. Kupffer and Biehringer have described for

the Field Vole and Water Vole respectively, the so-called "inversion of the germ layers," the reason for, and significance of, this "inversion" is now so well understood that I shall not do more than refer to this aspect of development in the water vole. Considerable space, however, is devoted to a description of the origin and significance of the giant cells which play such an important rôle in the placentation of Microtus.

CHANGES IN THE UTERINE TISSUES PRIOR TO ATTACHMENT

Externally little change is visible to indicate the presence of early developmental stages. A number of voles killed during the breeding season exhibited localised dilatations of the uteri, which suggested the presence of blastocysts, but examination of the ovaries and Fallopian tubes in section indicated that the uteri were not pregnant. In some cases the ovaries contained ripe follicles with undischarged ova, in others corpora lutea were present, but the eggs were still situated in the Fallopian tubes. Moreover, the ovary in the water vole is surrounded by a tough closed capsule which obscures the details and renders difficult the determination of the condition of the ovarian follicles when examined in the fresh or fixed state.

These localised dilatations of the uteri are indicative of changes undergone by the maternal tissues preparatory to the attachment of the embryos, hence it would appear that the sites of attachment of the blastocysts to the uterine mucosa are predetermined before the eggs reach the uteri at all.

Examination of these special areas of the uterus was rendered more difficult owing to the fact that after fixation and embedding the dilatations were no longer recognisable. Examination of many complete series of sections through uteri possessing these localised swellings demonstrated that the latter were due to a considerable increase in size and number of the superficial blood vessels. These vessels contract on fixation far more than the conjunctive tissue, hence it comes about that the uterus, which in the fresh state exhibited marked dilatations, appears after fixation to be of a more or less uniform diameter throughout, and those areas where the swellings occurred are only recognisable from the hypervascularity of the outer layers.

This increase in vascularity of the uterus is chiefly noticeable in the external layer of longitudinal muscle fibres and between it and the inner circular layer, where large blood sinuses occur. It seemed probable that these localised areas indicated the future sites of attachment of the eggs, and with a view to ascertaining the causes which conditioned the attachment at certain points and the fairly uniform spacing out of the embryos in the uteri, a large number of serial sections of uteri in which these local dilatations occurred, but in which the eggs had not reached the uteri, were examined in detail. The results were mainly negative; no definite changes could be detected either in the shape of the uterine lumen, or in the character of the lining epithelial cells, which marked off these areas as predetermined spots for the attachment of the eggs.

It is of course possible that these dilatations indicated the places where embryos were attached during a preceding pregnancy. From material collected, as this was, in the wild state, it is not possible to determine whether a female had already had young.

Many workers have studied this question which, however, still remains unanswered. Widakowich noted that the mucosa became more vascular before the attachment of the embryos occurred, but he apparently made no reference to the presence of local dilatations. He states, however, that cilia appear on certain areas of the uterine epithelium shortly after copulation and that they disappear after a short time. Other workers have confirmed this observation. I have not detected cilia either in the Fallopian tubes or uterine lumen of Microtus but it is possible that transitory ciliated areas occur.

It is not easy to imagine how cilia can cause the attachment of the eggs, but it is quite conceivable that they might prevent it. If that were the case one would expect to find large tracts of uterine epithelium provided with cilia and localised areas on the antimesometrial side devoid of them, the latter areas being the appointed places of attachment.

An alternative arrangement for arresting the eggs in certain regions of the uteri, and one moreover for which I have some slight evidence, is that in which the uterine epithelium contracts around the egg, closing above it temporarily until the remaining eggs are all attached. One can imagine that certain areas of the uterine epithelium on the antimesometrial side become hypersensitive, these hypersensitive areas corresponding to those of hypervascularity, and that they react to the presence of eggs in the lumen by closing above them. If such a condition obtains, then the eggs nearest the Fallopian tubes become enclosed first, the remainder passing over the enclosed eggs and becoming arrested in turn as they reach the successive sensitive areas.

The eggs while in the Fallopian tube are often crowded together, two or more often occurring in the same section, hence it is obvious that some such mechanism must exist in the uterus to prevent several embryos from lodging in one fold of the epithelial wall, for if such were to occur, it would be impossible for them all to reach maturity and examination of the ovaries of females in late stages of pregnancy reveals that there are no corpora lutea in excess of the number of developing embryos, hence one can assume that eggs do not become attached to the uterine epithelium so close together that one or more fail to develop.

An examination of the uterine epithelium in the neighbourhood of the blastocyst shown in Pl. XXV, fig. 1 reveals the fact that the latter is lying in a crypt or groove of the antimesometrial uterine lumen. Study of the serial sections in this region indicates that this groove was, at the time of preservation, or shortly prior thereto, shut off from the main lumen mesometrically to it. In fig. 1 a break is seen in the uterine epithelium on the right side, from which three or four cells have disappeared, while on the left side, there is, attached to the intact epithelium, a triangular mass consisting of these missing cells. This

clearly indicates that these epithelial layers were at one time in contact. The condition here figured is traceable in the sections over a distance of nearly ·4 mm.

One may therefore conclude that the crypt containing the blastocyst, becomes temporarily separated off from the remainder of the uterine lumen by the close adherence of the uterine epithelium forming its lips.

It might be suggested that this closure of the uterine lumen was an artefact, brought about by mechanical pressure after death. This, however, seems very improbable, for if such were the case, one would expect to find signs of lateral compression of the uterus in this region. No indications of such compression are recognisable; the diameter of the uterus in the region where this adhesion occurs is almost precisely the same as in other areas and the serous coat exhibits no signs of injury.

There is, moreover, collateral evidence that this adhesion was initiated prior to death, for the epithelial cells in that region are more columnar than those of the neighbouring portions of the epithelium. Pl. XXV, fig. 1.

SEGMENTATION OF THE OVUM

As has been described in a previous publication, the oocyte of Microtus gives off the first polar body while it is still in the Graafian follicle and this polar body divides mitotically into two. The outer wall of the follicle which has, by this time, become exceedingly thin, then ruptures and the secondary oocyte, surrounded by its zona and the cells of the corona radiata, passes into the fluid filled cavity of the capsule into which the fimbriated end of the Fallopian tube opens.

Unfortunately no stages of fertilisation were obtained, but from the fact that numerous sperms occur in the ovarian capsule it seems probable that fertilisation occurs therein. The oocyte, invested in its zona, then gives off the second polar body and passes into the Fallopian tube.

The first cleavage occurs in a plane at right angles to the plane of separation of the polar bodies and results in the formation of two blastomeres, which are apparently identical in size and character.

The average measurement of the two-celled egg is ·054 mm. × ·045 mm.; the thickness of the zona is ·003 mm. The latter, under minute examination, shows no signs of radial canals. In some of the two-celled stages in my possession there are indications of the presence of degenerating polar bodies lying underneath the zona in the cleavage plane, but in the majority of cases they are not recognisable.

No stages were obtained showing the completion of the second cleavage, but an ovarian segmenting egg, which has been described in a paper dealing with parthenogenetic cleavage in the water vole, shows the four blastomeres arranged in a cross shaped manner which is known to be typical of these rodents.

The second cleavage therefore probably results in the formation of the typical cross-shaped arrangement of the four cells, after which stage the segmentation appears to occur irregularly, for in the eight-celled stage, which measures ·074 × ·053 mm. there is no definite arrangement of the blastomeres. The zona is still intact and the cells appear similar in size and character, though had more precise cytoplasmic fixatives been employed, it is possible that some differentiation between the cells would have been recognisable. Unfortunately none of these eggs are really well preserved as they were fixed *in situ* in the Fallopian tubes.

Several stages with 12 or 13 cells were obtained. These morulae vary in size somewhat, the largest measuring ·074 × ·056 mm. and the smallest ·069 × ·056 mm. It will be seen therefore that during these early cleavages the egg has not materially increased in size. In the best preserved egg of this stage thirteen nuclei are present, one of which is situated in a central cell, which is, however, exposed to the surface on one side, thus suggesting a condition of epibole. This egg lies free in the upper portion of the uterus near the junction of the latter with the Fallopian tube; it has not yet reached its site of attachment. The zona is still present but appears to be in process of degeneration.

FORMATION OF THE BLASTOCYST

This irregular segmentation continues and leads to the formation of a more or less spherical blastocyst, having the form of a thin walled vesicle, at one side of which is a globular mass of cells projecting into the cavity (Pl. XXV, figs. 1 and 2). This mass of cells constitutes the embryonal knot and denotes, what I shall call, the upper pole of the egg, i.e. that portion which will become directed towards the mesometrium. The thin wall of the vesicle is the Trophoblast or extra-embryonal ectoderm; it is apparently at this stage quite distinct from, though in intimate contact with, the cells of the embryonal knot, at the upper pole of the egg.

The blastocyst shown in fig. 1 measures ·08 × ·07 × ·07 mm. of which the inner cell mass, or embryonal knot, measures ·05 × ·04 × ·04 mm. The one shown in fig. 2 measures ·09 × ·075 × ·06 mm., the embryonal knot ·05 × ·06 × ·04 mm. These blastocysts have apparently reached their definite sites of attachment to the uterus, but they are not yet correctly orientated although they are attached by a mucous secretion to the epithelium. These stages correspond in development to Sobotta's mouse egg at the end of the fourth day or Huber's rat egg of the fifth day after fertilisation.

The blastocyst represented in fig. 2 shows signs of differentiation of the cells of its embryonal knot into an outer layer of more or less uniform granular cells enclosing two rather larger cells, with pale staining less granular, cytoplasm. This apparent differentiation of the embryonal knot is not recognisable in the blastocyst shown in fig. 1, which is cut almost horizontally, the next section

of the series passing through the embryonal knot above the level of the blastocyst cavity.

It is, however, possible that the two pale-staining cells visible in Pl. XXV, fig. 2, are simply the products of a recent cell division. The two daughter cells resulting from a division are often rather different in appearance to neighbouring cells which have not so recently divided. The appearance of the nuclei in this case does not afford much guide.

The trophoblastic cells constituting the outer wall of the vesicle are somewhat elongated and flattened. Their cytoplasm is pale-staining and coarsely granular with ragged free surfaces.

At this time the uterine tissues exhibit very characteristic changes. The uterine lumen is wide and simple in character, the convolutions and diverticula, which are present prior to pregnancy, having disappeared in these regions where the blastocysts are located. The uterine glands are large but simple in character and their epithelium has undergone marked changes, the cells, normally columnar, are more cubical and the nuclei appear spaced out in a peculiar manner (Pl. XXV, fig. 1). This histological change is also recognisable in the uterine epithelium itself, but more especially in that portion of the anti-mesometrial wall neighbouring on the blastocysts. There the epithelial cells are very pale-staining and their nuclei small and widely separated, the cytoplasm around them appearing quite colourless and free from granularity.

In view of the fact that these cells are destined, at an early date, to degenerate and disappear, one might suppose that these histological changes were the preliminary processes leading up to that degeneration, but an examination of other sections in this, or in similar, series shows that tracts of uterine epithelial cells with identical characters occur in several other places, even on the mesometrial side of the lumen; it would appear therefore that these changes are in no wise conditioned by the presence of blastocysts in the uterus and that they do not necessarily indicate those regions in which the uterine epithelium is destined to disappear.

The connective tissue cells of the mucosa exhibit no marked change, but leucocytes are present in considerable numbers and capillaries are more numerous. As regards vascularity, however, by far the greatest change is noticed in the superficial layers of the uterus. Numerous and extensive blood vessels occur in the outer muscular coat. These vessels have contracted very considerably during fixation and subsequent treatment, with the result that the outer wall of the uterus has in most cases been thrown into numerous folds.

BLASTOCYST STAGES AND THEIR RELATIONS TO THE DECIDUAL CAVITY

The blastocyst, having reached its definitive position on the antimesometrial side of the uterine lumen, becomes orientated with its upper pole, containing the embryonal cell mass, directed towards the mesometrium. The

cells of the uterine epithelium, around the sides and lower pole of the blastocyst, flow together with the formation of a symplasma layer. This breaks down and disappears, with the result that the egg comes to lie in a narrow cleft, the implantation crypt, bounded laterally and antimesometrially, by the stroma cells of the uterine mucosa.

Text-fig. 1 illustrates this stage. The blastocyst lies in the implantation crypt, the opening of which into the narrow uterine lumen is closed by a plug of necrotic tissue, consisting of degenerating red blood corpuscles, leucocytes

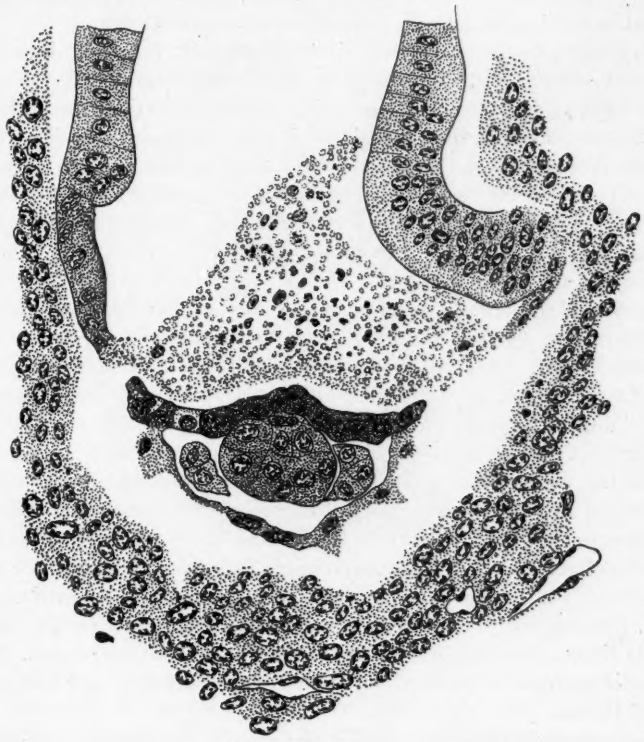


Fig. 1

and portions of symplasma derived from the uterine epithelium. The blastocyst, which has the form of a slightly flattened sphere, measuring ·11 mm. in transverse diameter and ·06 mm. in the future long diameter, consists of an outer trophoblastic layer, which is in contact at the mesometrial pole with a rounded mass of compact cells, which constitutes the embryonal knot. The cavity of the blastocyst is fairly extensive and contains several pale-staining cells which are mostly in close contact with the lower surface of the embryonal knot. These cells represent the future entoderm.

The outer wall of the vesicle appears to have contracted away from the uterine tissue during fixation or subsequent treatment. Its cells possess digitiform processes which during life no doubt penetrated into the spaces between the stroma cells. These irregular cells, constituting the outer wall of the blastocyst, serve to attach the latter to the maternal tissue lining the implantation crypt, they are usually regarded as purely trophoblastic in character and as being formed from the original trophoblastic wall of the unattached blastocyst. There is, however, a strong probability that in *Arvicola amphibius* the outer wall of the blastocyst at this time is not a purely embryonal structure, but that certain maternal cells have become incorporated in it.

Later, when dealing with the subject of giant cells, I shall produce evidence in support of this view, which appears at first sight improbable.

The cells of the mucosa surrounding the implantation cavity have lost their normal character, their nuclei are crowded together and cell outlines are in places unrecognisable. Numerous leucocytes are present, both in the superficial and deeper layers. The capillaries have increased in number to an enormous extent, particularly in the lateral and antimesometrial portions of the mucosa. A few of the endothelial lining cells of these capillaries are enlarged and stain very deeply.

The next stage in development is represented in text-fig. 2. The blastocyst measures ·074 × ·09 mm. and roughly corresponds to the six day rat embryo figured by Huber. The embryonal knot is distinctly separated from the covering layer of trophoblast. It has the form of a very compact ovoid mass of rather pale-staining cells measuring ·053 × ·04 mm. At the mesometrial end the covering trophoblast forms a curved disc, the margins of which bend upwards towards the mesometrium. It is in intimate contact with, but everywhere recognisable from the embryonal ectoderm and its constituent cells, which are cubical in character, stain more deeply than those of the latter. The margins of this trophoblastic plate extend outwards and upwards in contact with the uterine tissues of the implantation crypt, which communicates with the uterine lumen, mesometrially to it, by a comparatively narrow channel filled with necrotic tissue, degenerating epithelial cells and blood corpuscles. This trophoblastic plate is the primordium of the Träger of Salenka, or Ectoplacental Cone of Duval.

The parietal trophoblastic wall of the vesicle is continuous with the ectoplacental plate at its margins and extends around the implantation cavity in very intimate contact with the maternal tissue. It apparently consists of rather large irregular cells united by strands, but, as I have already stated, there is reason to believe that some at least of these cells are of maternal origin.

The entoderm has the form of a continuous layer of elongated, spindle-shaped cells, loosely investing the lower surface of the embryonal ectodermal mass. This layer of cells constitutes the visceral or inner yolk sac wall; between it and the ectoderm there are present one or two isolated cells which are

probably entodermal cells which have not become incorporated in the layer.

The differentiation of the uterine tissues has proceeded still further; the vascularisation of the outer, muscular layers has resulted in the formation of numerous and extensive blood sinuses between the longitudinal and circular muscle layers. From these sinuses many capillaries extend into the mucosa and give the latter, with the exception of that portion immediately surrounding the uterine lumen, a loose spongy character. The uterine glands are greatly reduced, both in size and number.

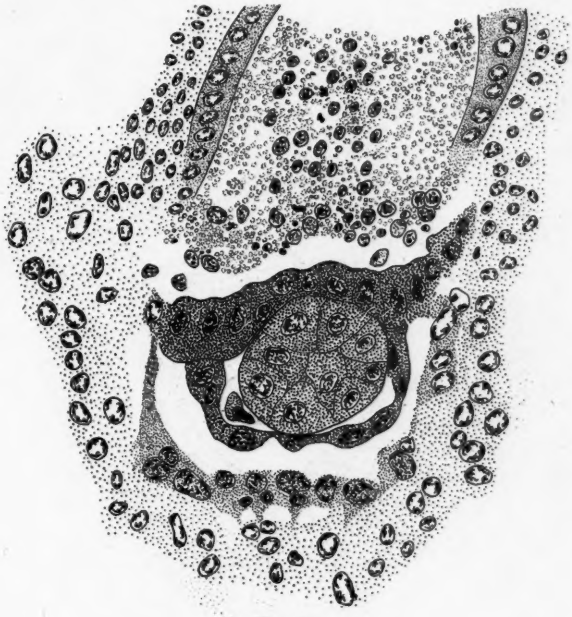


Fig. 2

This uterus, in the fresh state, exhibited well marked localised dilatations, corresponding, presumably, to the sites of attachment of embryos, but after sectioning, the variations in diameter, between the embryonal and inter-embryonal regions, were quite insignificant. The plications in the outer wall of the uterus indicated the extent of the contraction during fixation and subsequent treatment.

A considerable advance in embryonal development is shown in text-fig. 3 Here the blastocyst measures ·11 × ·11 mm., of which the embryonal ectodermal mass measures ·04 × ·04 mm. The ectoplacental trophoblast or Träger has thickened at its edges, where it is in contact with the walls of the implantation cavity, and appears to be in a state of active proliferative growth. The

ectodermal mass has the form of an almost spherical solid structure composed of rather pale-staining cells. The entoderm, in this stage, forms a closed vesicle, consisting of elongated, deeply-staining spindle-shaped cells with ovoid nuclei. The upper wall of this entodermal vesicle is applied to the lower surface of the ectodermal mass and constitutes the visceral yolk-sac wall; it is continuous with the parietal yolk-sac wall which is at this time intact, the yolk-sac cavity being shut off from the cavity of the blastocyst. This outer yolk-sac entoderm is destined to disappear as an intact layer at an early date, though its cells continue to divide and remnants of the layer persist throughout the whole gestation period.

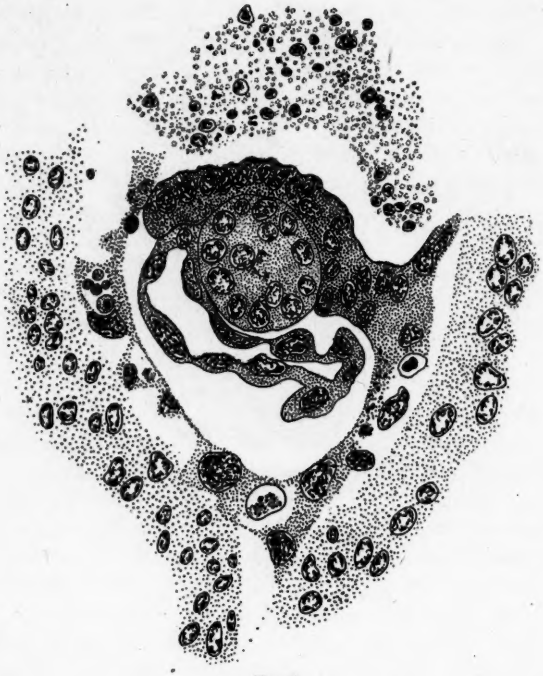


Fig. 3

The peripheral or parietal wall of the vesicle consists, over its extent, of a single layer of large cells with very vacuolated cytoplasm united by fine strands. The nuclei of these cells are, on the average, far larger than those of the ectoplacental trophoblast and their cytoplasm is prolonged into irregular processes which pass into the decidual tissue surrounding the implantation cavity. These cells appear to be actively phagocytic, for many red blood corpuscles and dark-staining granules are present in them.

Similar cells, at the antimesometrial end of the early blastocyst, have been described by Sobotta, Duval and Melissinos in the Mouse, and by Widakowich

and Huber in the Rat. Considerable discussion as to their significance has taken place; I shall revert to this question when describing the origin of the placental giant cells.

The next stage in development is represented in text-fig. 4. The blastocyst now measures ·16 mm. in length and ·11 mm. in diameter. The embryonal ectodermal mass measures ·048 × ·048 × ·06 mm. The ectoplacental trophoblast

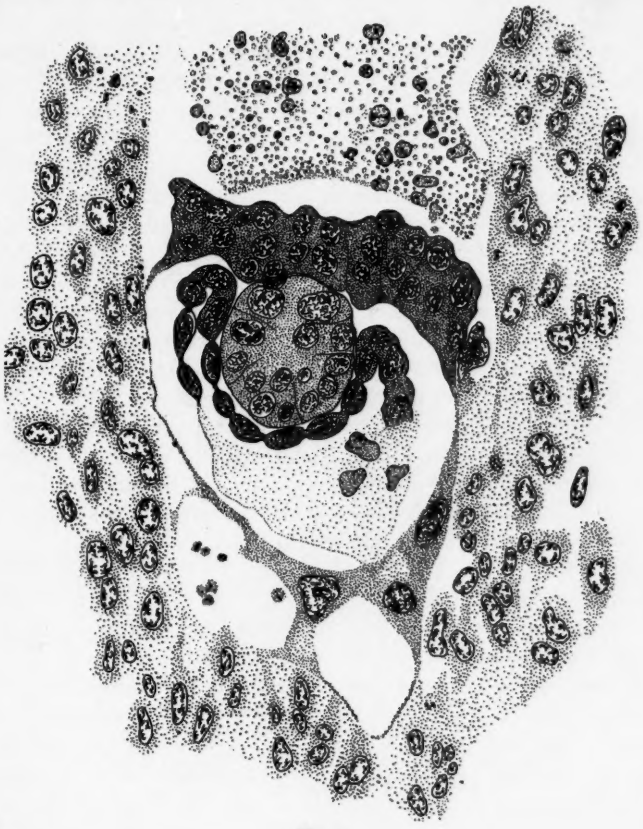


Fig. 4

has the form of a slightly curved plate of deeply-staining cells, considerably thicker than in the preceding stage. Marginally it is continuous with a fine structureless membrane which is in contact with the wall of the implantation cavity. This membrane, which represents the parietal trophoblastic wall of the blastocyst, is Reichert's membrane. In intimate union with this membrane are large cells with vacuolated cytoplasm, similar to those described in the last stage.

The embryonal ectoderm has the form of an almost spherical solid mass of pale-staining cells in contact with, but sharply marked off from, the ectoplacental trophoblast. The increase in thickness of the latter over its middle region has forced the embryonal ectoderm downwards into the cavity of the blastocyst, with the result that the underlying layer of entoderm has become invaginated. This visceral or splanchnic entoderm is mostly in close contact with the lower surface and sides of the embryonal ectoderm. It consists of a single layer of very regular, dark-staining, spindle-shaped cells with ovoid nuclei. At the point of junction of the ectoplacental trophoblast and embryonal ectoderm this layer is reflected downwards into the cavity of the blastocyst as the parietal entoderm, but it no longer constitutes a continuous membrane. Over the lateral walls of the cavity it is complete and its cells similar in character to those of the visceral layer, but around the lower pole of the blastocyst it has already broken down and is only represented by a few scattered cells. These cells, however, continue to divide and form an attenuated layer in contact with Reichert's membrane.

The maternal tissues have undergone further changes. The cells of the mucosa around the implantation cavity have increased in size and assumed the character of typical decidual cells. They are compactly grouped together and cell outlines are in many places unrecognisable. Numerous capillaries are present in these masses of decidual cells, and their endothelial lining cells are often large and darkly staining. The implantation cavity is still in open continuity with the uterine lumen, but the epithelium of the latter shows signs of degeneration over a considerable area at the antimesometrial end, the cell walls having disappeared with the formation of a symplasma layer, which is destined to degenerate at an early date.

Between the stages already described and that represented by text-fig. 5 there is, unfortunately, a considerable gap in the material, but a stage which we possess of the Field Vole, the development of which appears to agree closely with that of the Water Vole, serves to bridge the gap fairly well.

The blastocyst in question has the form of an elongated hollow cylinder measuring ·55 mm. in length and ·15 mm. in diameter. It corresponds roughly with that represented by Huber's fig. 27*c* of the eight day rat embryo.

One can distinguish three areas of this egg cylinder. First a hemispherical, cup-shaped, region at the antimesometrial end, constituted by the embryonal ectoderm. The cells forming the wall of this deep cup, which appears almost horse-shoe shaped in vertical section, are very closely crowded together and are in a state of active proliferation, numerous mitoses being present. The lips of this cup are in continuity with, but fairly sharply defined from, the extra-embryonal ectoderm which constitutes the middle region of the egg cylinder. There the cells are less crowded together than in the embryonal region and mitoses, though present, are far less numerous. At the mesometrial end this layer passes rather abruptly into the tissue of the Träger, which is, by this time, a cone-shaped structure of considerable size, composed of rather large

pale-staining cells with almost spherical nuclei. The cells of the Träger are irregularly disposed in groups, between which are present masses of maternal blood corpuscles. The Träger projects upwards into the still persistent uterine lumen the epithelium of which has disappeared in the antimesometrial portion,

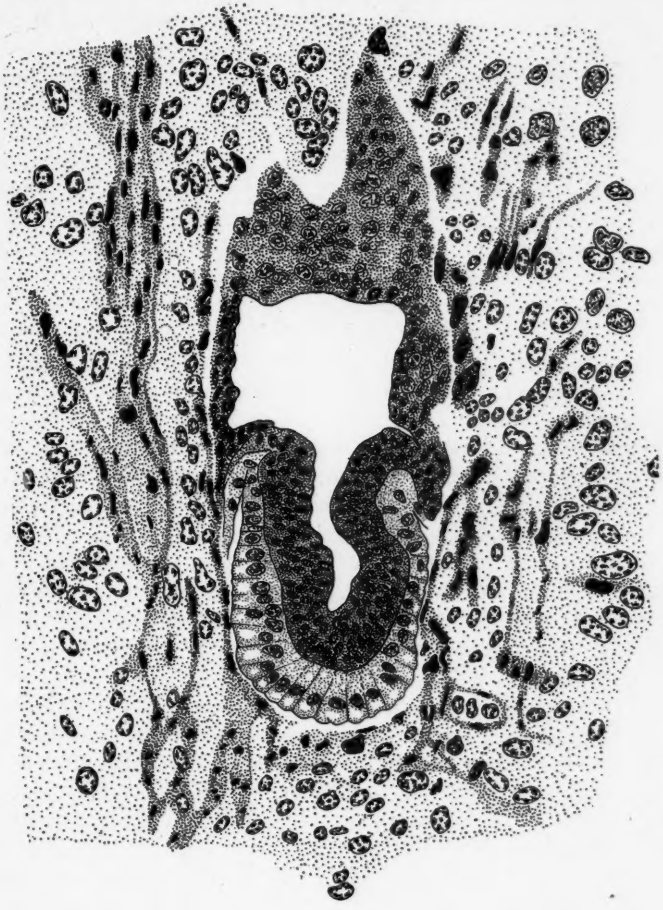


Fig. 5

while over the remainder, with the exception of a small area at the mesometrial end, it has broken down with the formation of a symplasma layer. Mingled with the cells of the advancing edge of the Träger are a number of large cells united by cytoplasmic filaments. The spaces between these cells, and the cytoplasm of the cells themselves, contain maternal blood corpuscles, which also occur amongst the trophoblastic cells of the Träger. These cells, which are

in reality small giant cells, are held by some workers to be trophoblastic in origin, but as will be seen later they are actually of maternal origin.

The parietal trophoblastic wall of the egg cylinder is continuous at the mesometrial end with the cells of the Träger, but it has the form of a thin structureless membrane in intimate contact with the walls of the implantation cavity. This membrane—Reichert's membrane—has adherent to its inner surface a few scattered isolated cells, mostly fusiform in shape, which represent the parietal yolk-sac entoderm.

The egg cylinder itself is clothed externally by a layer of splanchnic or visceral entoderm. Over the embryonal ectodermal cup it has the form of a single layer of fusiform or ovoid cells, constituting the embryonal entoderm, whilst over the extra-embryonal ectoderm it is composed of very large columnar cells, in which the nuclei are situated basally. The cytoplasm of these cells is very coarsely granular and in places vacuolated, but I cannot detect the haemoglobin granules which Sobotta described and figured in the outer portions of the cells of the visceral entoderm in the Mouse. As this layer approaches the mesometrial end of the cylinder the cells become more cubical in character and at the junction of the extra-embryonal ectoderm and the Träger it disappears as a continuous membrane and is only represented by the scattered cells in contact with Reichert's membrane, referred to above.

As regards the maternal tissues, a considerable advance in differentiation has taken place. All the cells of the mucosa antimesometrially and laterally to the implantation cavity have become converted into typical decidual cells with large vesicular, pale-staining, nuclei. These masses of decidual cells are penetrated by numerous extensive blood sinuses, the endothelial cells of which are large and deeply-staining. Around the walls of the implantation cavity and extending upwards therefrom, in contact with the symplasma layer formed from the degenerating uterine epithelium, is a belt of deeply-staining spindle-shaped cells with dark elongated nuclei. These cells I regard, for reasons which I shall state later, as the endothelial cells of maternal capillaries, the lumina of which have disappeared owing to apposition of the vessel walls.

Coming now to the stage of *Arvicola amphibius* represented by text-fig. 5, we find the blastocyst completely embedded in maternal tissue, the uterine lumen being restricted to a very narrow passage, with fine radial canals, at the mesometrial side of the decidual swelling. It measures ·3 mm. in length and ·15 mm. in breadth and is of the cylindrical form, characteristic of rodents with inversion of the germinal layers.

The ectoplacental cone is now greatly enlarged and consists of a mass of rather pale-staining cellular tissue and is of irregular shape, being prolonged into digitiform processes which extend upwards into the decidual tissue mesometrially to it. The nuclei of these trophoblastic cells are smaller than those of the maternal cells and react to stains in a rather different manner. The Träger forms the roof of a cavity of considerable size, the primitive amniotic cavity, which later becomes subdivided into the amniotic cavity

proper and the ectoplacental or false amniotic cavity. The embryonal ectoderm now has the form of a deep cup, the lip of which is continuous with the tissue of the Träger, its walls being composed of narrow columnar cells which increase in number towards the lower pole, where the layer is considerably thicker. Externally, this embryonal ectoderm is invested by the splanchnic yolk-sac entoderm, which consists of a single layer of long columnar cells with pale-staining vacuolated cytoplasm. The inner ends of these cells are often densely granular, but here again, I am unable to detect the presence of haemoglobin granules. At the junction of the embryonal ectoderm and the trophoblast, the entoderm is reflected back, but it almost immediately loses its character as a distinct cell layer and is only represented by a few scattered cells lying in contact with the outer wall of the vesicle formed by Reichert's membrane. This now has the form of an exceedingly thin structureless membrane, in intimate contact with, and difficult to distinguish from, the maternal tissues lining the implantation cavity. These tissues have by this time undergone marked changes. An intense cell proliferation has taken place around the implantation cavity with the result that the decidual swelling has become converted into a compact tissue, composed of large cells, with rather pale-staining nuclei, subdivided by numerous fine blood channels lined by endothelium. The lumina of these capillaries are often exceedingly narrow, indeed the endothelial walls are frequently so closely apposed that the lumen appears completely obliterated. The nuclei of these endothelial cells are long and narrow, stain intensely dark with haematoxylin, whilst the cell cytoplasm stains deeply with eosine. These narrow capillaries, with their modified endothelial lining, form a very well marked annular zone around the implantation cavity, and a belt of these cells constitutes the actual lining of the cavity around the antimesometrial end and lateral regions of the embryo. They are apparently fused with Reichert's membrane, with the result that the latter is scarcely recognisable.

It will be seen from the above that this early blastocyst of Microtus differs somewhat from the corresponding stage of the Mouse and Rat. In the latter forms, the ectodermal cylinder is completely invested, except at the upper pole, by the splanchnic yolk-sac entoderm, whereas in *Microtus amphibius* the junction of the embryonal ectoderm and the trophoblast, i.e. the region from which the amnion folds will later arise, marks the limit of upward extension of the yolk-sac entoderm. In later stages, however, this condition no longer obtains. The visceral entoderm gradually extends in a mesometrial direction, so that a similarity with the typical murine condition is re-established.

The next stage available is represented in Pl. XXV, fig. 3. The blastocyst measures 1·4 mm. in length and ·63 mm. in diameter, excluding the trophoblast of the Träger, the limits of which are difficult to determine for purposes of measurement. The blastocyst now exhibits the form typical for rodents with inversion; it contains three extensive cavities: the one nearest the meso-

metrium is purely trophoblastic and constitutes the false amniotic or ectoplacental cavity. Its roof is continuous with the tissue of the Träger; its floor, together with a layer of mesoderm, constitutes the roof of the extra-embryonal coelom, the so-called "chorion." Its lateral walls are clothed externally with a layer of splanchnic entoderm, the visceral yolk-sac wall having, by now, extended upwards almost to the junction of the Träger with the lateral walls of the ectoplacental cavity. The middle and largest cavity of the blastocyst is the extra-embryonal coelom, which is lined by an exceedingly fine layer of fusiform mesodermal cells. Its roof, as already described, consists of a layer two or three cells thick of cubical trophoblastic cells, lined internally with mesoderm, and constitutes the "chorion." Its lateral walls are clothed with columnar entodermal cells, while the floor, which is extremely thin, is constituted by the amnion, consisting of two closely apposed fine layers of ectoderm and mesoderm. The embryonal ectoderm has the form of a thick curved plate, the medullary plate, composed of elongated columnar cells. The visceral entoderm in which the vesicle is invested is not of the same character throughout. Below the embryonal ectoderm the entodermal cells are partly cubical, partly fusiform and constitute a thin compact layer. In the middle region of the egg cylinder, around the extra-embryonal coelom, the entoderm consists of very tall columnar cells, in which the nuclei are situated basally. The cytoplasm of these cells is vacuolated, coarsely granular, and prolonged into irregular processes. This layer gradually thins down as it approaches the Träger, and before reaching the latter it is reflected back as the parietal yolk-sac wall, which is represented by isolated cells, lying in contact with Reichert's membrane. The latter is continuous with the tissue of the Träger at its margins and forms a very distinct lining to the implantation cavity; it has already increased somewhat in thickness as compared with the previous stage and would appear to have a protective function. It prevents the passage of maternal blood, particularly leucocytes, into the yolk-sac cavity, and limits the destructive and phagocytic activities of the giant cells or megalokaryocytes to the maternal tissues. It persists throughout the gestation period and increases very considerably in thickness in later stages.

The uterine swellings in which the embryos are situated are at this stage of considerable size. They are egg-shaped, the narrow end, in which the embryo is located, being antimesometrial in position. They average 4 mm. in diameter and 5·5 mm. in length (Pl. XXV, figs. 3 and 4).

The original uterine lumen on the mesometrial side has almost disappeared, being represented by an exceedingly fine passage, but its former connection with the implantation cavity is usually marked by an extensive blood sinus, which serves to assist the rapid penetration of the foetal trophoblast of the Träger. The decidual tissue is everywhere extremely vascular. On the mesometrial side, the cells are small and densely crowded together, with numerous large blood sinuses lined by endothelium. On the antimesometrial side the cells are large and pale-staining, having the character of typical decidual cells;

blood sinuses are equally abundant, but far smaller than those at the mesometrial end. The implantation cavity itself is considerably larger than the embryonal formation, the space between Reichert's membrane and the decidua being occupied by extensive blood lacunae, enclosed in the meshes of a fine network, the strands of which are united by very large cells with densely-staining nuclei. The origin and nature of these cells is discussed later.

I do not propose to describe the further development of the embryo, or the origin of the mesoderm, as detailed accounts of the development of other rodents are available and from the rather limited number of stages of Microtus at hand, it is not possible to follow the development in detail. I shall therefore proceed to describe the placentation, and origin of the placental giant cells.

PLACENTATION AND ORIGIN OF THE GIANT CELLS

The general character of the placentation in *Arvicola amphibius* does not appear to differ markedly from that of the Rat or Mouse, and the ripe placenta is very similar. In all three forms the blastocyst comes to lie excentrically in a crypt on the antimesometrial side of the uterine lumen. The uterine epithelium surrounding it degenerates and disappears, with the result that the trophoblastic wall of the vesicle is brought into direct contact with the stroma of the uterine mucosa. The cells of the latter immediately around the blastocyst become destroyed by the agency of giant cells, while those more remote become converted into decidual cells. The ectoplacental trophoblast at the mesometrial end of the blastocyst thickens rapidly and grows forwards through the uterine tissues which thus become penetrated by a coarse network of trophoblastic cells, which destroys the endothelial lining of the maternal blood vessels. The blood extravasations thus formed become enclosed in trophoblastic tissue. At a later stage the mesodermal allantois fuses with the "chorionic" mesoderm underlying the trophoblast and when vascularisation of the allantois is initiated, the allanto-chorionic mesenchyme, carrying foetal capillaries, extends into the trophoblast, which by this time has the form of a complex system of lamellae, honeycombed with narrow channels in which the maternal blood circulates. In this way the definitive allantoic placenta is established.

Although the placentation of *Arvicola amphibius* is similar to that of other murine rodents, there are considerable differences in detail.

Before describing the development of the placenta, however, it seems desirable to give an account of the origin of the giant cells.

Origin of the Giant Cells.

A very characteristic feature of Rodent placentae is the presence of numerous large cells, Riesenzellen, Megalokaryocytes or Giant Cells as various authors have designated them. They occur abundantly in the Rat, Mouse and Field Vole but do not appear to attain the number or dimensions that they do in the placenta of the Water Vole.

If one examines a section through the fairly late placenta, such as is represented in Pl. XXXII, fig. 27, one sees that the margins of the placental disc consist almost exclusively of these giant cells, while very many others occur in the decidual tissues, particularly in the region just beyond the limit of penetration of the trophoblast, that is to say, in the area which has been termed the "Umlagerungszone." These giant cells make their appearance soon after the egg has become attached to the uterine tissues, and a considerable time before the allantoic outgrowth is recognisable. In stages corresponding to that represented in Pl. XXV, fig. 3, one finds a few large isolated giant cells of very considerable size embedded in the decidual tissues, not necessarily adjacent to the implantation cavity, in fact often close to the muscularis.

The question as to the origin of these cells has occupied the attention of a number of workers but the conclusions arrived at are by no means in agreement.

According to Jenkinson, Duval, Sobotta and Hubrecht, these giant cells are of foetal origin, being derived from the trophoblast. These writers affirm that certain cells of the parietal trophoblast of the early blastocyst, become detached, penetrate the maternal tissues, and grow in size by ingulfing decidual cells and maternal blood.

According to Disse, who worked on *Arvicola arvalis*, the giant cells are purely maternal in derivation. He states that they appear prior to the attachment of the egg to the uterine epithelium and that their origin from maternal tissue is therefore beyond question. He ascribes their formation to some stimulus, derived from the fertilised egg, but in no wise limited to the immediate neighbourhood of the egg, since large giant cells and symplasma masses occur deep down in the uterine tissues, far from the implantation cavity. The course of events according to Disse is as follows: Some stimulus from the fertilised egg causes certain maternal cells to flow together with the formation of symplasma masses, while others increase in size, by ingulfing decidual cells and symplasma masses already formed, until they come into contact with the walls of maternal capillaries. They destroy the endothelial walls and pass into the lumen of the vessels, whence they are carried to the implantation cavity and deposited on the wall thereof. In this way, Disse explains the presence of the giant cell network which surrounds the embryonal formation in the earlier stages and which persists around the margin of the placenta throughout the whole period of gestation.

Disse supports his statements with numerous figures representing these Riesenzellen ingulfing decidual cells, symplasma masses and maternal blood. He also shows them in contact with, and, according to him, destroying, by phagocytosis, the endothelial walls of maternal capillaries and ultimately lying free in the lumen of the vessels.

Otto Grosser, in his more recent description of the placenta of the Rat, expresses agreement with the observations of Duval and Sobotta. He states that cells from the transitory trophoblastic wall of the vesicle penetrate the

mucosa and grow into giant cells, which serve to enlarge the implantation cavity by destroying the decidual cells which constitute its wall. According to him, the superficial layer of the trophoblast of the Träger also becomes, in later stages, converted into giant cells and constitutes the Umlagerungszone. He says:

"In etwas späteren Stadien (figs. 118 and 119) ist diese Veränderung der peripheren Trägerzone gleichfalls kenntlich; von Degeneration der Zellen ist aber nur mehr wenig zu sehen, die Zellen sind in intensiver resorbierender Tätigkeit begriffen und vielfach mit aufgenommenen mütterlichen Blutkörperchen beladen. Die Zellen sind bedeutend grösser als die übrigen Trophoblastelemente, sie wandeln sich in die Riesenzellen älterer Placenten um." He holds, however, that a certain number of giant cells are of maternal origin being formed from decidual cells which, under the influence of the invading trophoblast, flow together with the formation of symplasma masses: "Unter seinem (Träger) Einfluss, der vielleicht anfänglich mehr in einer Fermentwirkung wie in einem aktiven Vordringen der Zellen besteht, gehen die oberflächlichen Deciduaschichten zugrunde, zum Teil nach Symplasmabildung (mütterliche Riesenzellen)."

Jenkinson, in his account of the histology and physiology of the placenta of the Mouse, also supports the trophoblastic origin of the giant cells.

All these workers are of opinion that the giant cells are essentially migratory in character. Sobotta, Duval, Jenkinson and Grosser maintain that they migrate from the trophoblastic wall of the vesicle into the decidua, while Disse, on the other hand, maintains that they are formed in the decidua remote from the blastocyst and migrate to the wall of the implantation cavity.

My own observations on the placenta of *Arvicola amphibius* do not confirm either of these theories. I am in agreement with Disse as regards the maternal character of these giant cells but differ from him as to their time of first appearance and as to their origin. There is, moreover, no evidence that these cells in the placenta of Microtus are migratory.

In the stage represented by text-fig. 5 the implantation cavity is surrounded by an annular zone of tissue which, owing to its peculiar reaction to stains, is sharply differentiated from the remainder. It consists of a belt of maternal capillaries, the lumina of which are greatly reduced, with the result that the endothelial walls are almost in apposition. The cytoplasm of these endothelial cells stains intensely with eosine, while the nuclei stain black with haematoxylin.

Capillaries with such a modified endothelial lining are present in many parts of the decidual swelling, but they reach their maximum number in the area surrounding the lateral walls of the implantation cavity.

It is these endothelial cells, I maintain, which give origin to the giant cells or megalokaryocytes of the Microtus placenta.

Figs. 5–16 (Pls. XXVI, XXVII and XXVIII) are reproductions of photomicrographs illustrating the successive stages in giant cell formation. They are not selected from progressive developmental stages, since it is unnecessary to do

so, for the transformation of endothelial cells into giant cells is a continuous process, which lasts until the placenta is fully formed. It is moreover a rapid metamorphosis, for quite large giant cells are present in early stages such as Pl. XXV, fig. 3.

Pl. XXVI, fig. 5 represents a portion of the decidual capsule around the embryo shown in text-fig. 5. The dark coloured strands are endothelial cells lining maternal capillaries, the lumina of which are greatly reduced. The cells are somewhat enlarged and their cytoplasm stains intensely with eosine.

In Pl. XXVI, fig. 6 is shown, under a higher magnification, one of these capillaries traversing typical decidual tissue. It will be seen that the endothelial lining is quite intact but that many of the cells have undergone characteristic changes. Their nuclei stain intensely dark and are considerably enlarged. The cytoplasm is increased in amount and appears fibrillar.

In Pl. XXVI, fig. 7 is seen an enlarged capillary or sinus, the endothelial wall of which is everywhere recognisable yet in which certain cells have increased enormously in size. The nuclei are large and vesicular with irregular black chromatin masses and fine reticulum. The cytoplasm is finely fibrillar in character with very irregular ragged free surfaces.

In Pl. XXVI, fig. 8 is shown a similar stage. The cells though profoundly changed are still unmistakably endothelial. The deeply-staining cytoplasm, which formed the characteristic annular zone around the implantation cavity in text-fig. 5, is clearly visible.

A later stage is represented in Pl. XXVII, fig. 9; here the cells have increased in thickness and their outer surfaces are in more intimate contact with the surrounding decidual cells; it is in fact difficult to determine their limits, for their cytoplasm is prolonged into irregular processes which pass between the neighbouring cells.

In the next stage, Pl. XXVII, fig. 10, the cells have increased in size still further and are unmistakably giant cells, yet they still retain their endothelial character.

In Pl. XXVII, fig. 11, but for the fact that the enlarged cells form a more or less continuous layer, enclosing a space filled by maternal blood, one would hardly recognise them as transformed endothelial cells. Their cytoplasm is vacuolated and in many cases contains fragments of decidual cells and blood corpuscles.

The maximum development is shown in Pls. XXVII and XXVIII, figs. 12 and 13. Their cytoplasm is coarsely fibrillar, vacuolated and contains much foreign matter. The cells remain quite distinct from one another, they do not form a syncytium or symplasma, the cell outlines between neighbouring giant cells being clearly defined, but where their cytoplasm comes into contact with decidual tissue it appears to be actively phagocytic, ingulfing the decidual cells and symplasma masses formed therefrom. Numerous brown granules are present around the periphery of some of these cells (Pl. XXVIII, fig. 14). They possibly represent a haemoglobin derivative, for numerous red blood

corpuscles in various stages of degeneration are present in the cytoplasm. These cells are actively phagocytic, their cytoplasm usually containing large vacuoles and fragments of maternal cells. The fixatives employed have not permitted me to determine the occurrence of fat and glycogen.

The giant cells apparently attain their maximum size in the outer regions of the uterine tissues (Pl. XXVIII, fig. 15), where one occasionally finds isolated cells measuring as much as ·3 mm. in length, quite close to the muscularis. It is, however, around the embryonal formation that the giant cells are most abundant (Pls. XXVIII, XXIX and XXXII, figs. 16, 17 and 27). Here they constitute a vascular network, the meshes of which contain maternal blood. This network makes its appearance quite early. In the stage represented by Pl. XXV, fig. 3 the blastocyst is already surrounded by a belt of tissue which consists almost entirely of giant cells united by strands enclosing maternal blood. These large blood lacunae are therefore not extravasations, as they are commonly called, since their containing walls are of purely endothelial origin. As no injections were carried out I am unable to determine whether the blood, during life, circulates through the meshes of this network, but there is no reason to suppose that it does not. The maximum development of this vascular network is shown in Pl. XXVIII, fig. 16, and Pl. XXXII, fig. 27. Its innermost layer comes into contact with Reichert's membrane and the cytoplasmic filaments of its individual cells come into actual organic continuity therewith. The outer layer of giant cells is in contact with the maternal decidual cells which, under the influence of these phagocytic cells, flow together to form irregular, deeply-staining, symplasma masses. Pl. XXIX, figs. 17 and 18 show the formation of such symplasma from decidual cells in proximity to the megalokaryocytes. Ultimately these symplasma masses are ingulfed and absorbed by the giant cells, as shown in Pl. XXIX, figs. 19 and 20, with the result that, all the decidual tissue around the lateral walls and antimesometrial end of the embryonal formation, is replaced by giant cells. As the embryo increases in size, this giant cell network becomes stretched and its constituent cells become very attenuated, so that in later stages, such as that represented by Pl. XXXI, fig. 25, the yolk-sac splanchnopleur is only separated from the regenerated uterine epithelium by a thin layer composed of Reichert's membrane and the flattened giant cells. Around the margin of the placental disc, however, this stretching process is strictly limited, with the result that the giant cell network persists in this region and its cells increase in size; hence in later stages the giant cells are most conspicuous in the placental margin (Pl. XXXI, fig. 25 and Pl. XXXII, fig. 27).

The function of these giant cells would appear to be twofold. In the first place they serve, by their destruction and absorbtion of the maternal tissues, and by their resulting growth in size, to surround the implantation cavity with an exceedingly vascular spongy tissue, which permits and facilitates expansion of the embryo and which, constituting as it does the maternal portion of the yolk-sac placenta, also facilitates the nutrition of the embryo. In the

second place, these cells serve as purely destructive agents which ingulf maternal tissues. As the embryo increases in size, a very considerable amount of maternal tissue must be removed from the lateral and antimesometrial portions of the decidua and there is probably a decided advantage in employing, for this phagocytic purpose, the same agents as are employed for increasing the vascularity of the implantation cavity wall, and agents, the life of which is moreover strictly limited.

With regard to those giant cells which are sometimes found close to the muscularis, and which attain a diameter of ·3 mm. (Pl. XXVIII, fig. 15), it is not clear what useful purpose they can serve, but their position may be more or less accidental, as we have no knowledge of those processes which condition the conversion of normal endothelial cells into megalokaryocytes. An isolated endothelial cell of some superficial blood vessel, if it once started its metamorphosis into a giant cell, might be expected to grow more rapidly than one surrounded by other giant cells, for in the latter case the food supply would of necessity be more limited. There is, as I have already stated, no evidence that these giant cells are migratory and I regard the presence of these isolated cells as an indication that migration does not take place, for if it did, these cells would probably make their way to the wall of the implantation cavity. The presence of giant cells in the placental labyrinth itself also points to the fact that they are not migratory. The advance of the foetal trophoblast into the maternal tissues is aided by the presence of giant cells which destroy the decidual cells and increase the vascularity of the tissues. These giant cells are surrounded by the trophoblast and apparently remain at their places of origin even when the allanto-chorionic villi penetrate the latter.

Although Disse studied *Arvicola arvalis* it is of interest to note that many of the figures which accompany his paper might have been drawn from my own preparations. His figs. 7 and 17 which, according to him, represent giant cells destroying by phagocytosis the walls of maternal blood lacunae prior to entering the blood stream, can be interpreted as large isolated endothelial cells. The fact that the endothelial lining is absent where in contact with the Riesenzellen indicates that the latter are derived from constituent cells of that endothelium.

Although Hubrecht later maintained that giant cells were of trophoblastic origin, yet his observations on Erinaceus support my view, for he remarked on the thickened endothelium of the maternal vessels and stated that it gave origin to a layer of bulky cells, with conspicuous nuclei, surrounding the blastocyst and enclosing spacious blood lacunae. The large individual units of this layer he called Deciduofracts. Finally, he suggested a possible homology between the Deciduofracts of Erinaceus and the giant cells of Rodents.

If this explanation which I have put forward of the origin of placental giant cells is applicable to other types such as the Field Vole, Rat and Mouse, it is remarkable that the earlier workers did not consider its possibility. Duval, in his account of the Rodent placenta, noticed that many sinuses containing maternal blood were lined by large cells, which he interpreted as trophoblastic.

According to him the trophoblast creeps up the walls of the maternal vessels destroying the endothelial lining and forming a pseudo-endothelium of trophoblastic origin which he termed the "couche plasmodiale endovasculaire." Jenkinson, in his more recent account of the Mouse placenta, criticised this statement as follows: "It seems to me obvious that his (Duval's) 'endovascular plasmodium' is nothing else but the lining of a trophoblastic sinus in the upper, glycogenic, portion of the placenta. In other words he is absolutely correct in attributing an embryonic origin to the cells which form the lining of these cavities, totally incorrect in regarding the cavities themselves as maternal." Jenkinson himself, apparently, had no doubt that these cells were trophoblastic, for he states: "The glycogenic tissue is traversed by sinuses leading into the sinuses which pass directly through the placenta, and, like these, lined by a pseudo-endothelium of flattened trophoblastic cells. These cells are always larger than the endothelial cells of the maternal tissues (figs. 35 and 39); they frequently project boldly into the lumen of the sinus and in fact may become almost large enough to deserve the name of megalokaryocytes."

Maximow, on the other hand, does not agree with this view for he states that the "couche plasmodiale endovasculaire" of Duval is simply an hypertrophied condition of the endothelial cells, which, according to him, later become infiltrated with leucocytes and destroyed.

It is of interest to note that in certain pathological conditions analogous changes, in the character of endothelial cells, occur.

Dr J. A. Murray has drawn my attention to the Report of the Tuberculosis Commission for 1911, in which Eastwood describes and figures certain changes in endothelial cells under the influence of tubercle bacilli. The report, which is exceedingly lengthy, contains the following passages:

"In early infections it is constantly found that the endothelial cells of the affected area become swollen. This change must be attributed to some diffusible irritant associated with the presence of bacilli; it is not confined to the endothelial cells with which bacilli are actually in contact. Swollen endothelial cells often become detached and pass into the fluid contained within the endothelial lining. They then present the appearance of what are sometimes called 'macrophages'" (p. 279).

"Associated with the swelling up of those endothelial cells which are in direct contact with bacilli, there are changes in the nucleus. The nucleus generally stains more darkly than the normal, and the material taking this stain often stains diffusely and tends to escape into the surrounding protoplasm" (p. 279).

"Whilst these nuclear changes are going on there is also to be observed a dissolution of continuity in the protoplasmic outline and a tendency of the endothelial protoplasm to fuse with the protoplasm of contiguous parenchymatous or other cells" (p. 280).

"A further stage in the process which is frequently observed is that these groups of nuclei continue, for a time, to multiply; they then form large groups which, taken in conjunction with their protoplasmic environment, are termed giant cells" (p. 163, sect. (3)).

In connection with the above it is perhaps significant that the cytoplasm

of the placental giant cells stains diffusely with basic dyes, e.g. haematoxylin, and tends to fuse with the cytoplasm of decidual cells in contiguity with it. Pl. XXVII, figs. 9, 10, 11, and 12.

It appears therefore that some stimulus derived from the fertilised egg causes the endothelial cells of the capillaries, in the embryonal regions of the uterus, to grow into phagocytic giant cells. It is probably correct to attribute this stimulus to the embryo and not to the corpus luteum, since the endothelial cells in the inter-embryonal areas retain their normal character.

There remains for discussion the question of the significance of the large cells which are present at the antimesometrial end of the early blastocyst, referred to on page 342. The interpretation of these cells is by no means easy.

Sobotta described these cells at the antimesometrial end of the 6 days blastocyst of the Mouse and held that they were giant cells derived from the parietal trophoblast and that they served for the attachment of the blastocyst to the uterine tissues and, by their phagocytic activity, brought about extravasations of blood for the nourishment of the embryo.

Melissinos, on the other hand, maintained that the cells in question owed their apparent size to the fact that, through the shrinkage of the blastocyst during preservation, they are seen in sections in surface view and not in profile. Widakowich also noted these cells and accepted the explanation of their appearance put forward by Melissinos. Huber, in his more recent description of the development of the Albino Rat, supported this interpretation.

In *Arvicola amphibius* I am unable to accept the view that the size of these cells is apparent and not real, for the following reasons:

(*a*) The nuclei are considerably larger in all dimensions than those of the trophoblastic cells in other regions, measuring ·015 × ·02 × ·02 mm., as compared with ·01 × ·008 × ·01 mm.

(*b*) The cells in this region of the blastocyst remain the apparent largest throughout the whole series of sections, whereas if their apparent size were due merely to superficial cutting, they might well be expected to appear of normal dimensions in other sections.

(*c*) In horizontal sections through the implantation cavity, they still appear larger than the remainder.

Hitherto all workers are agreed that these large antimesometrial cells are trophoblastic; their identity does not appear to have been questioned. I venture to suggest, however, that they are maternal in origin, and that they are true giant cells, derived from endothelial cells in precisely the same way as the large megalokaryocytes of the placenta.

The question of the derivation of these cells is intimately bound up with a second one, namely, the mode of origin and growth of Reichert's membrane, and it must be admitted at the outset that it is almost impossible to demonstrate clearly, either by drawings or photomicrographs of sections of early blastocysts, that these cells are of maternal origin, since they frequently appear to be actually constituent cells of the vesicle wall. But this structure-

less membrane, whether it be regarded as a product of the parietal trophoblast of the early vesicle, or as a basement membrane laid down by the cells of the parietal entoderm, in later stages comes into most intimate connection with the giant cells and is then, undoubtedly, no longer a purely embryonal structure, for it increases enormously in thickness in that region where the giant cell network persists, i.e. around the margin of the placental disc, and processes of the giant cells fuse with it and are identical in appearance with it (Pl. XXX, fig. 23).

Moreover maternal leucocytes collect in large numbers outside this membrane, which undoubtedly serves to prevent the passage of leucocytes into the yolk-sac cavity, yet a certain number are actually embedded in its substance. This is strong evidence that the increase in thickness of this membrane is brought about through the agency of giant cells, for it is difficult to conceive how leucocytes, which are initially outside the membrane, can become encapsuled in it, if the latter is being added to on its inner surface. If, therefore, we admit that this membrane is partly the product of giant cells, it is not unreasonable to suggest that cells found in structural continuity with it in early stages, are actually maternal giant cells, and further that they are phagocytic endothelial cells.

If one examines the decidual tissue close around the antimesometrial end of the early blastocyst, one finds numerous capillaries, many of the endothelial cells of which are undergoing the initial changes which ultimately lead to the formation of giant cells. This change is probably due, as suggested above, to some stimulus derived from the egg, therefore one would expect to find it most evident in those endothelial cells which come into actual contact with the wall of the blastocyst. It seems exceedingly probable therefore, that these large cells, which form part of the outer wall of the early blastocyst and which have given rise to the view that some at least of the placental giant cells are of trophoblastic origin, are themselves of maternal origin.

With regard to the origin of the giant cells in the placenta of the Mouse.

I am of opinion that the giant cells arise in the same manner as in Microtus, and that the suggested homology between these cells and the Deciduofracts of Erinaceus is a true one. Although Hubrecht's description of the placentation of the Hedgehog, in which he makes this suggestion, was published 33 years ago, no worker seems to have confirmed it. This is remarkable because the work of Disse in 1906 and of Pujiula in 1908 established the fact that giant cells were derived from maternal tissues, whereas up till then most authorities were of opinion that the Deciduofracts of Erinaceus were trophoblastic in origin.

I have had no opportunity of examining the placenta of Erinaceus, but judging from Hubrecht's very detailed description and excellent figures, it seems clear that a change in the character of the endothelial cells occurs similar to that which has been described herein for Microtus. It should be noted that, in the Mouse, the change in character of the endothelial cells in

early stages, corresponding to text-figs. 4 and 5, is far less marked than in Microtus; this is probably in correlation with the fact that the placental giant cells are far less numerous in the Mouse. In the Field Vole however, they are at least as marked as in the Water Vole. I hope at some future date to describe the origin of the giant cells in the Field Vole.

DEVELOPMENT OF THE PLACENTA

Placentation is initiated on the foetal side by the outgrowth and active proliferation of the trophoblast covering the upper pole of the blastocyst, the ectoplacental cone or Träger, and on the maternal side by the conversion of the uterine epithelium mesometrially to the egg, into a symplasma layer which rapidly disappears, with the result that the trophoblast is brought into contact with the sub-epithelial tissue. The latter is exceedingly rich in capillaries, the endothelial cells of which, in the neighbourhood of the implantation cavity, undergo those preliminary changes which lead ultimately to the formation of phagocytic giant cells. These endothelial cells often lose continuity with one another, with the result that blood extravasations take place into the uterine lumen mesometrially to the embryo. The foetal trophoblast grows rapidly upwards into this extravasation, losing, as it does so, its original compact pyramidal form and assuming the character of a coarse cellular network, enclosing in its meshes maternal blood.

At the same time a rapid metamorphosis of endothelial cells into giant cells takes place around the lateral walls and antimesometrial end of the implantation cavity. The giant cells thus formed ingulf the neighbouring decidual cells and enlarge the implantation cavity which in this way comes to be surrounded by a network of giant cells, the strands of which are of endothelial origin, and the meshes of which are filled with maternal blood. This belt of highly vascular tissue comes into intimate contact with the outer wall of the blastocyst, which consists of a fine structureless membrane derived from the original trophoblastic wall of the vesicle. Strands from the giant cells fuse with this membrane and are indistinguishable from it. The Träger, which is at first cone shaped in vertical section, extends rapidly in the lateral direction; thus increasing the area of attachment to the maternal tissues. Its penetration is greatly assisted by the activity of the giant cells, which not only ingulf and resorb the decidual cells but which also increase the vascularity of the tissue into which the trophoblast will extend. The development has now reached the stage represented by Pl. XXV, fig. 3, in which it will be seen that the blastocyst is surrounded by extensive blood lacunae the limiting walls of which are formed by the endothelial giant cells. The section shown in this figure does not pass through the Träger.

In the meantime the primordium of the allantois makes its appearance as an almost solid outgrowth of mesodermal cells at the level of the junction of the amnionic fold with the medullary plate (Pl. XXV, fig. 3). As development proceeds the allantois increases in size and grows upwards through the extra-

embryonal coelom as a pear-shaped structure, the distal half of which is vesicular in character, i.e. it contains a fluid filled cavity, whilst the proximal portion consists of loosely packed stellate mesenchymatous cells. *Pari passu* with this growth of the allantois, the extra-embryonal coelom increases markedly in size, apparently under the influence of internal pressure, with the result that the chorionic roof is forced upwards until it comes into contact with the overlying trophoblast of the Träger (Pl. XXV, fig. 4).

This contact between the "chorion" and trophoblast is first initiated over the middle region as the result of which the ectoplacental or false amniotic cavity becomes restricted to an annular space, the external diameter of which corresponds roughly with the diameter of the Träger at its base. The "chorion" consists of a single layer of more or less cubical trophoblastic cells invested on its lower surface by an exceedingly attenuated mesodermal membrane in which the nuclei are widely separated and filiform in character. The trophoblastic cells of the "chorion" are apparently identical in character with and, after fusion has taken place, indistinguishable from, those of the Träger.

At the stage of development represented by Pl. XXV, fig. 3 the trophoblast is purely cellular, there is no differentiation into a cytotrophoblast and syncytiotrophoblast; moreover, it does not appear to be actively phagocytic; owing to the activity of the endothelial giant cells, the decidual tissue mesometrially to the Träger is largely resorbed with the result that the advancing edge of the trophoblast is preceded by a belt of giant cells and maternal blood. It should be noted, however, that this belt of giant cells, which probably corresponds to the "zone of ingrowth" or "Umlagerungszone" of the Rat, is not itself migratory. It is formed *de novo* in successive regions, always slightly in advance of the ingrowing trophoblast, which latter therefore comes to enclose in its meshes, not only maternal blood, but also endothelial giant cells. In these early stages many of the trophoblastic lacunae possess an endothelial lining, which soon, however, degenerates, though deeply-staining masses which represent the giant cell nuclei are recognisable for a considerable time. In the lateral regions and around the antimesometrial side of the embryonal formation similar changes in the maternal tissues are in progress. Immediately outside Reichert's membrane there is established a vascular giant cell network containing maternal blood. The decidual tissues adjacent to this zone become converted into multinucleate symplasma masses (Pl. XXIX, fig. 17) which are ingulfed and resorbed by the giant cells (Pl. XXIX, fig. 20). Similar symplasma masses are formed from the decidual cells mesometrially to the "zone of ingrowth."

An embryo at this stage possesses five pairs of mesodermal somites. The allantois measures 1·5 mm. in length and ·45 mm. in diameter at its distal vesicular end. The vesicular portion is at present quite devoid of blood vessels, but the presence of foetal vessels in the embryonal mesenchyme, adjacent to the attachment of the allantoic stalk, indicates that vascularisation will shortly take place.

Unfortunately no stages were obtained in which the first union of the allantois with the "chorion" was taking place, but it seems probable that by the time the vesicular portion has reached the trophoblast its vascularisation is completed. In the next developmental stage available it is seen that the area of allanto-chorionic union is almost as wide as the area of the decidua into which the trophoblast has penetrated. This wide area of union is doubtless correlated with, if not actually conditioned by, the vesicular character of the allantois, for it is clear that a more rapid flattening can take place in the case of a vesicle than in that of a solid sphere.

Immediately this layer of vascular allantoic mesenchyme has come into contact with the chorionic mesenchyme, the formation of foetal villi sets in. It appears, as Jenkinson has pointed out for the Mouse, that the overlying chorionic trophoblast is not merely invaginated into the trophoblast of the Träger by the upgrowth of the allantoic mesenchyme, but that it takes an active part in the process of ingrowth. In the case of the Mouse, however, the trophoblast of the Träger is already syncytial, constituting the "plasmodi-trophoblast," whereas in Microtus the trophoblast retains its cellular character until the penetration of the allantoic villi has set in. In these early stages of placental formation it is therefore possible to distinguish three regions in the foetal portion of the placenta. Firstly an irregular zone of actively proliferating cellular trophoblast beyond the region of penetration of the allantois. Secondly a zone of syncytial trophoblast into which the foetal villi have penetrated. Thirdly a zone of cellular trophoblast, which Jenkinson calls the "cyto-trophoblast," which is simply the floor of the original ectoplacental cavity. This cellular trophoblast very soon becomes perforated by the allantoic villi, with the result that the latter come into direct contact with the syncytial layer. The ingrowth of the allantoic villi results in the formation of a series of thin trophoblastic syncytial lamellae, containing maternal blood, separated by mesenchymatous villi carrying foetal capillaries. In this way the definitive allantoic placenta is established (Pl. XXXII, fig. 27).

From now onwards throughout the gestation period the changes in the placenta are purely of the nature of an elaboration of pre-existing structure.

In vertical sections through the placental disc of stages similar to, and more advanced than, that represented by figs. 25 and 27 three well defined zones are recognisable. The zone nearest the mesometrium consists of typical decidual tissue penetrated by wide blood lacunae, the endothelial lining cells of which are in various stages of conversion into giant cells, those nearest the ingrowing trophoblast being usually considerably more advanced in their metamorphosis, with the result that the decidual tissue in this region becomes converted into a syncytium which is resorbed by the giant cells. The middle zone of the placental disc consists of the actively proliferating cellular trophoblast, in which are embedded numerous giant cells and masses of maternal blood.

The third zone is constituted by the placental labyrinth consisting of

trophoblastic syncytial lamellae honeycombed with channels, in which the maternal blood circulates, alternating with mesenchymatous villi carrying allantoic capillaries. Attached to the syncytial walls of the lamellae are numerous small giant cells, which have apparently remained at their places of origin on the vessel walls and become surrounded by the trophoblastic syncytium.

It seems clear that the "Umlagerungszone" of Grosser, which according to him is formed by the conversion of the superficial layer of the trophoblast into giant cells, is, in Microtus, represented by the irregular layer of giant cells formed from the endothelial cells lining the maternal blood sinuses in proximity to the ingrowing trophoblast.

According to Duval, the trophoblast creeps up the walls of these maternal sinuses, destroys the endothelial lining and forms a pseudo-endothelium of syncytial trophoblast which he termed the "couche plasmodiale endovasculaire." Jenkinson's interpretation of Duval's figures representing this endovascular plasmodium, differs somewhat. He agrees with Duval that the cavities are lined by trophoblast, but maintains that they are not maternal sinuses. He considers that they are simply spaces in the foetal trophoblast containing extravasated maternal blood.

There is little doubt that in Microtus these sinuses are maternal and that their containing walls are modified endothelial cells.

As development proceeds the proliferation of the cellular trophoblast fails to keep pace with the ingrowth of the foetal villi, with the result that the placental labyrinth increases in thickness at the expense of the middle layer. In the nearly ripe placenta the cellular trophoblast, which formerly constituted the middle zone, is only represented by comparatively small islands of tissue surrounded by giant cells, blood lacunae and decidual cells.

THE YOLK-SAC PLACENTA

The yolk-sac placenta in Microtus, as in other rodents with inversion of the germ layers, plays a subsidiary rôle in the nutrition of the embryo. Owing to the character of development, the yolk-sac cavity early comes into open continuity with the cavity of the blastocyst (text-fig. 4). At this time the entoderm cells constituting its persistent visceral wall are ovoid and simple in character, but by the time the blastocyst has reached the "egg-cylinder" stage they exhibit a differentiation which indicates that they are engaged in resorbtive activity (text-fig. 5).

The entodermal cells around the embryonal ectoderm first become columnar, their cytoplasm exhibits vacuolation, their free surfaces being granular and apparently engaged in absorbing nutrient fluid from the yolk-sac cavity. As already stated, there is no evidence in the case of Microtus that these cells contain haemoglobin. No maternal blood can reach the yolk-sac cavity, which remains throughout gestation shut off from the maternal tissues by Reichert's

membrane, and any substance absorbed by the entodermal cells of the yolk-sac splanchnopleur must have passed by osmosis through this membrane.

It is of interest to note that these entodermal cells attain their maximum size and activity, below the embryonal ectoderm, quite early in development (text-fig. 5), whereas at a rather later stage, such as is represented in Pl. XXV, fig. 3, they have become reduced in size in this region and form a layer of cubical or flattened cells, which do not appear to be absorbtive at all, whilst on the other hand the cells covering the extra-embryonal coelom and ectoplacental cavity have become tall and columnar.

At a time when the embryo possesses about five somites, vascularisation of the yolk-sac splanchnopleur sets in, and concurrently therewith there are developed folds and villi, in that portion of the splanchnopleur which is adjacent to the placenta (Pl. XXV, fig. 4).

As development proceeds these entodermal folds increase in size and complexity and omphalopleural vessels penetrate into them (Pl. XXX, fig. 22).

These villous folds attain their maximum size over the margins of the placental disc, whereas on the antimesometrial side the entoderm has the form of a simple layer of columnar cells in close contact with Reichert's membrane. Apparently, this villous portion of the yolk-sac splanchnopleur is concerned with the absorbtion of nutritive material, which has diffused into the yolk-sac cavity from the annular zone of vascular giant cell tissue, which encircles the placenta proper.

At a stage corresponding to that shown in Pl. XXXI, fig. 25, the uterine lumen has been reformed on the antimesometrial side of the capsularis, and the yolk-sac splanchnopleur is only separated from the uterine cavity by a comparatively thin layer, consisting of Reichert's membrane, the network of attenuated and degenerating giant cells, and a thin layer of circular muscle fibres. As the embryo increases in size the capsularis becomes stretched still further, until, in very late stages, it is represented by a thin membrane composed of the now flattened cells of the yolk-sac splanchnopleur closely applied to Reichert's membrane.

According to Jenkinson and Grosser, this layer ruptures a considerable time before birth, with the result that the yolk-sac splanchnopleur becomes exposed to the uterine lumen. In *Arvicola amphibius* this does not occur, for in the latest stage which I possess, where the uterine swellings measure 16 mm. in diameter and the placenta 13 mm. × 3·5 mm., the splanchnopleur and Reichert's membrane are still intact.

Owing to the fact that the Water Vole material was collected in the wild state, it is not possible to ascertain the age of this foetus, but it is clear from its size and condition that it is close on full time.

It is worthy of note, therefore, that Reichert's membrane persists throughout the gestation period, or at all events, until parturition is imminent.

SUMMARY

1. The development of *Microtus amphibius* is of the excentric type. It agrees in general outlines with that of the Mouse and Rat.

2. The implantation cavity early becomes surrounded by a belt of maternal capillaries, the endothelial cells of which exhibit characteristic changes.

3. These endothelial cells become phagocytic giant cells. The decidual tissue adjacent to them breaks down with the formation of symplasma masses, which are resorbed by these giant cells.

4. All the placental giant cells are of maternal endothelial origin. The trophoblast does not contribute to their formation, as has been described in the Mouse and Rat.

5. The ectoplacental trophoblast does not appear to be actively phagocytic. Its penetration is assisted by the giant cells, which destroy the decidual tissue in its line of advance.

6. Around the antimesometrial end, and lateral walls, of the implantation cavity, the giant cells form a vascular network in contact with Reichert's membrane. This network serves to facilitate the rapid stretching of the capsularis which results from growth of the embryo.

7. The trophoblast of the Träger retains its cellular character until the penetration of the allanto-chorionic mesenchyme has set in, and even then the formation of syncytio-trophoblast is limited to that portion in contact with, or adjacent to, the allantoic villi.

8. The ripe placenta is of the discoidal, haemo-chorialis type, the maternal blood circulating in syncytial trophoblastic lamellae, subdivided by foetal mesenchymatous villi, carrying allantoic capillaries.

9. The yolk-sac splanchnopleur does not come into contact with maternal tissues until parturition, or very shortly prior thereto. It is always separated therefrom by the persistent Reichert's membrane.

REFERENCES TO LITERATURE

Assheton, R. (1905). "On the foetus and placenta of the Spring Mouse." *Proc. Zool. Soc.* London. vol. II.

—— (1895). "The attachment of the mammalian embryo to the walls of the uterus." *Quarterly Journ. Micros. Sci.* vol. XXXVII.

Bernard (1859). "Sur une nouvelle fonction du placenta." *Comp. Rend. Acad. Sci.* Paris.

Biehringer, J. (1888). "Ueber die Umkehrung der Keimblätter bei der Scheermaus." *Archiv f. Anat. und Phys.*

Bischoff, T. "Entwicklungsgeschichte des Meerschweinchens." *Abhand. der math. naturwiss. Classe der König. bayrisch. Akad. der Wissenschaften.*

Burckhard, G. "Die Implantation des Eies der Maus in die Uterus-schleimhaut und die Umbildung derselben zur Decidua." *Archiv f. mikr. Anat.* Bd. LVII.

Disse, J. (1906). "Die Vergrösserung der Eikammer bei der Feldmaus." *Archiv f. mikr. Anat.* Bd. LXVIII.

Duval, M. (1889–1892). "Le placenta des Rongeurs." *Journ. de l'Anat. et de la Phys.*

FRASER, A. (1882). "On the Inversion of the blastodermic layers in the Rat and Mouse." *Proc. Roy. Soc.* No. 223.

FROMMEL (1888). *Über die Entwicklung des Placenta von Myotus murinus.* Wiesbaden.

GROSSER, O. (1909). *Die Eihäute und der Placenta.* Wien.

HUBER, G. C. (1915). "The Development of the Albino Rat, *Mus norvegicus albinus.*" Memoirs of the Wistar Institute of Anatomy and Biology. *Journ. Morphol.* vol. XXVI. No. 2.

HUBRECHT (1889). "Studies in mammalian embryology. (I) The Placentation of Erinaceus." *Quart. Journ. Micros. Sci.* vol. XXX.

—— (1908–9). "Early Ontogenetic phenomena in mammals." *Quart. Journ. Micros. Sci.* vol. LIII.

JENKINSON, J. W. "Observations on the histology and physiology of the placenta of the Mouse." *Tijd. Neder. Dierk. Ver.* II, dl. vii.

KUPFFER, C. (1882). "Das Ei von *Arvicola arvalis* und die vermeintliche Umkehr der Keimblätter an demselben." *Sitz. Ber. Akad. d. Wiss.* II. Kl.

MELISSINOS, K. (1907). "Die Entwicklung des Eies der Mäuse." *Arch. f. Mikr. Anat.* Bd. LXX.

OCHS, A. (1908). "Die intrauterine Embryonalentwicklung des Hamsters bis zum Beginn der Herzbildung." *Zeitsch. f. wiss. Zool.* Bd. LXXXIX.

PUJIULA, D. (1908). "Die Frage der Riesenzellen bei der Entwicklung der Maus." *Actas y memorias del Primer Congreso de Naturalistas Españoles.*

REICHERT (1861). "Beiträge zur Entwicklungsgeschichte des Meerschweinchens." *Abhand. d. Akad. d. Wiss.* Berlin.

ROBINSON, A. (1892). "Observations upon the development of the segmentation cavity, the archenteron, the germinal layers, and the amnion in mammals." *Quart. Journ. Micros. Sci.* vol. XXXIII.

SALENKA, E. (1883–4). *Studien über die Entwickelungsgeschichte der Thiere.* Wiesbaden.

SOBOTTA, J. (1903). "Die Entwicklung des Eies der Maus vom Schlusse der Furchungsperiode bis zum Auftreten der Amniosfalten." *Arch. f. Mikr. Anat.* Bd. LXI.

—— (1903). "Die Entwicklung des Eies der Maus vom ersten Auftreten des Mesoderms an bis zur Ausbildung der Embryonalanlage und dem Auftreten des Allantois." *Arch. f. Mikr. Anat.* Bd. LXXVIII.

VON SPEE (1901). "Die Implantation des Meerschweineis in die Uteruswand." *Zeitschr. Morph. Anthrop.* Bd. III.

WIDAKOWICH, V. (1909). *Über die erste Bildung der Körperform bei Entypie des Keimes.* Leipzig.

DESCRIPTION OF PLATES XXV—XXXII

Fig. 1. Transverse section through a uterus containing an unattached egg. The characteristic change in the character of the uterine epithelial cells is clearly visible. × 200.

Fig. 2. An early stage similar to the above. Localised changes in the epithelial cells of the uterine lumen at the antimesometrial end are visible. × 200.

Fig. 3. Longitudinal vertical section through a uterus containing an early blastocyst. The section does not pass through the Träger. × 15.

Fig. 4. Transverse section through a uterus containing an embryo with about five somites. The ectoplacental cavity is obliterated, except around its margins, by the union of the "chorion" with the trophoblast. The vesicular character of the allantois is well shown. × 15.

Fig. 5. Section through the maternal tissue near the implantation cavity, in a stage corresponding to text-fig. 5 or fig. 21. The deeply stained strands are endothelial cells lining narrow maternal capillaries. × 150.

Fig. 6. A higher power view of the same tissue traversed by a fine capillary, the endothelial cells of which are beginning their metamorphosis into giant cells. × 360.

Fig. 7. Section through the placenta, showing a large maternal blood vessel. The endothelial cells are greatly enlarged. × 360.

Fig. 8. Section through the decidual tissue in which may be seen a maternal capillary, the lining of which has undergone hypertrophy. × 360.

Fig. 9. Section through the decidua showing a maternal vessel. Three endothelial cells have become giant cells. Their outer surfaces, which abut against the decidual cells, have fused therewith. × 360.

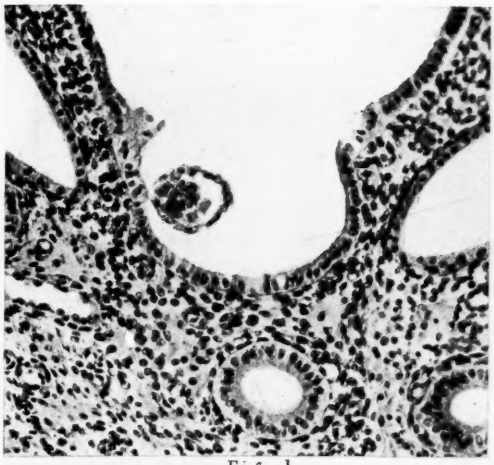


Fig. 1.

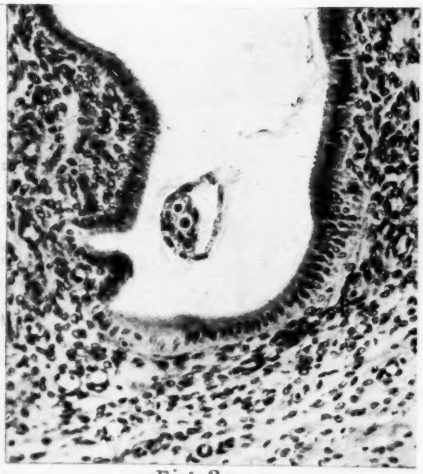


Fig. 2.

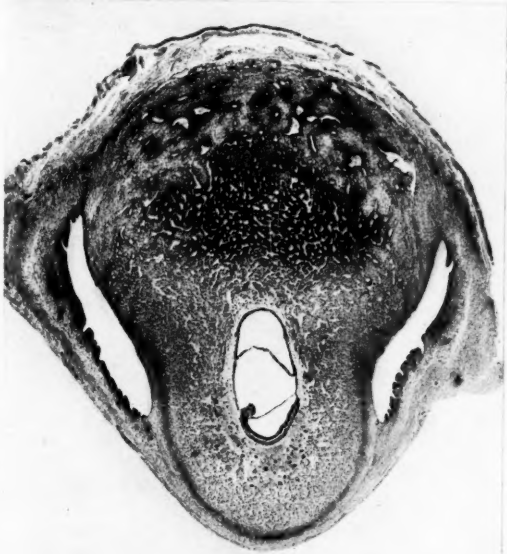


Fig. 3.

Fig. 4.

UNIV. OF MICH.

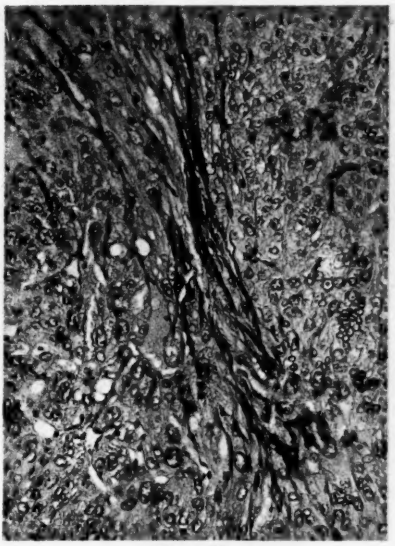


Fig. 5.

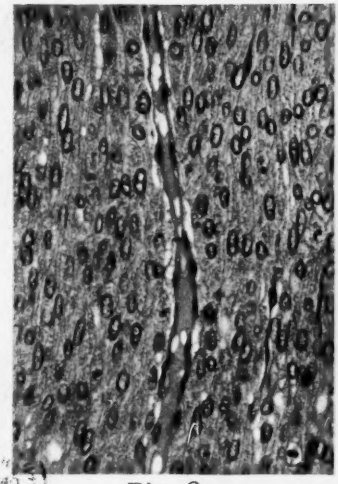


Fig. 6.

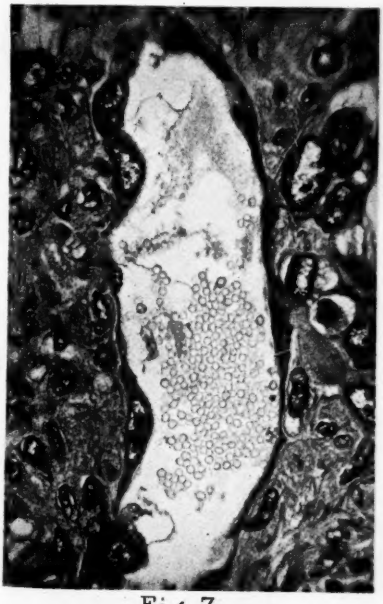


Fig. 7.

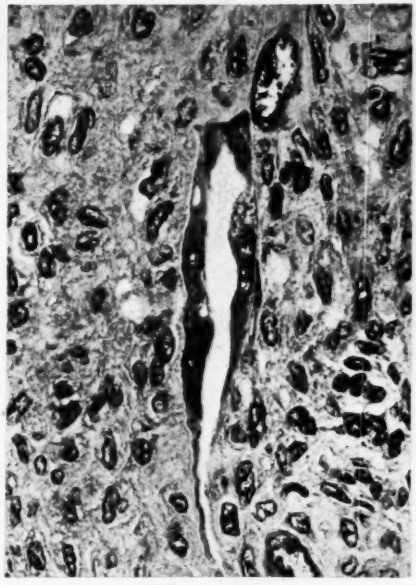


Fig. 8.

UNIV. OF MICH.

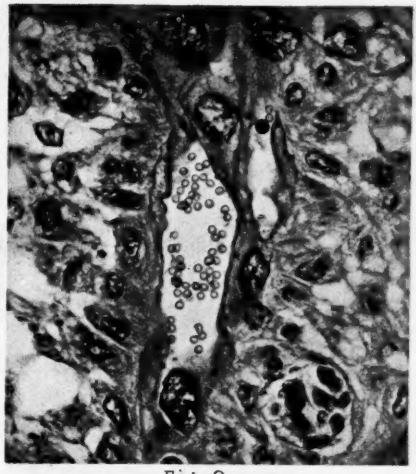


Fig. 9.

Fig. 10.

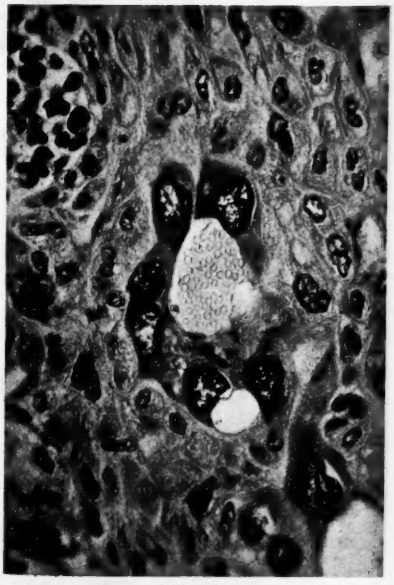


Fig. 11

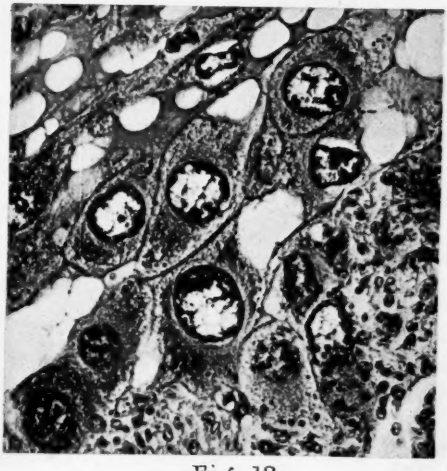


Fig. 12.

UNIV. OF MICH.

Fig. 13.

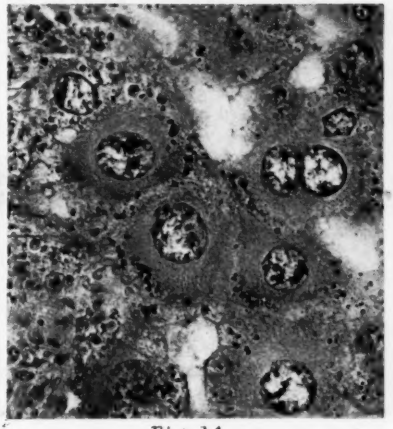


Fig. 14.

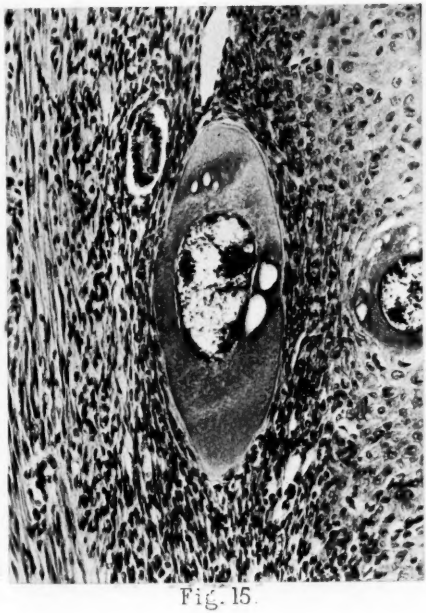


Fig. 15.

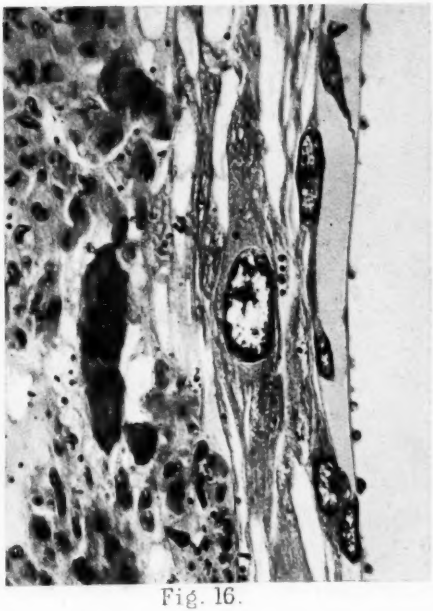


Fig. 16.

UNIV. OF MICH.

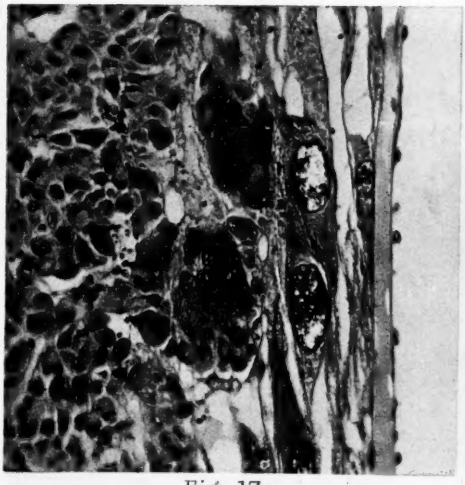


Fig. 17.

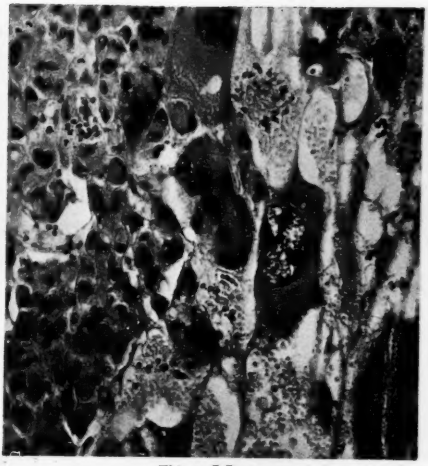


Fig. 18.

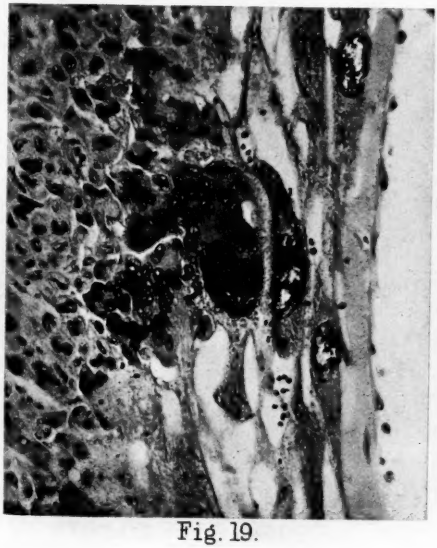


Fig. 19.

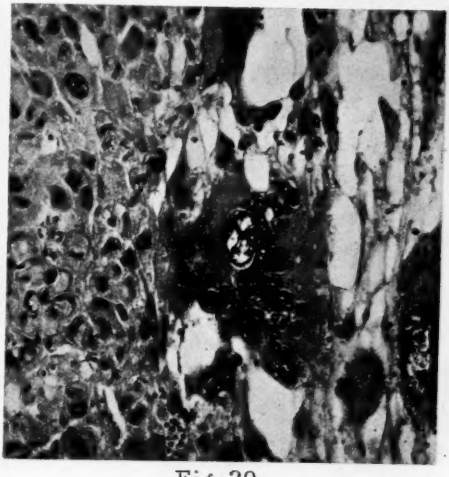


Fig. 20.

UNIV. OF MICH.

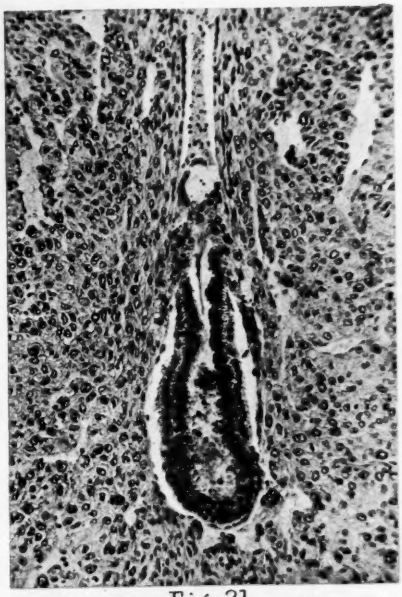


Fig. 21.

Fig. 22.

Fig. 23.

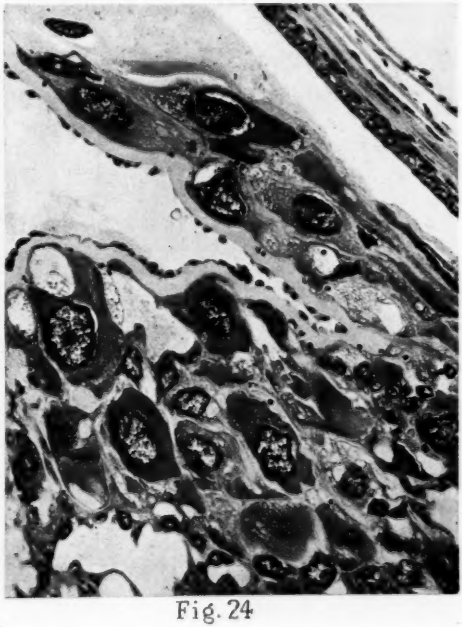


Fig. 24

UNIV. OF MICH.

Fig. 25.

UNIV. OF MICH.

Fig. 26.

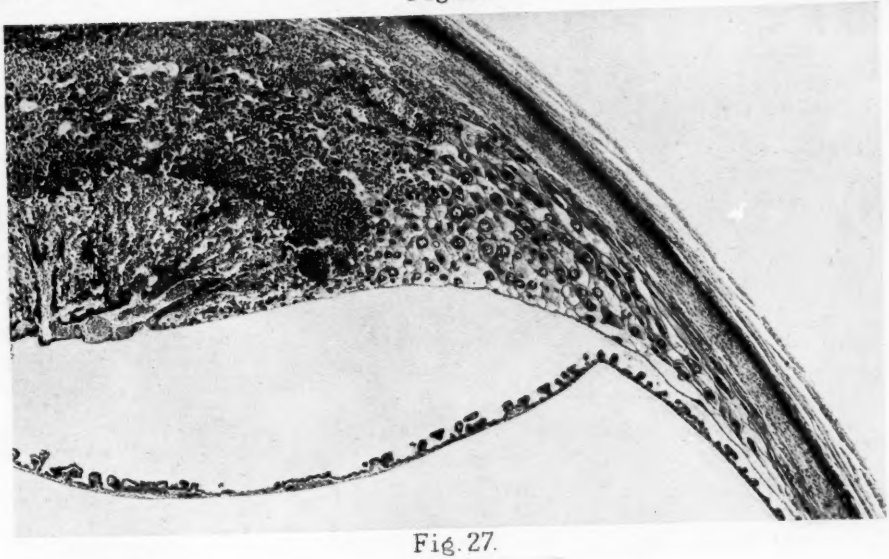


Fig. 27.

UNIV. OF MICH.

Fig. 10. Section through the decidual tissue, showing a large maternal blood sinus, the endothelial cells of which are typical giant cells yet retain their endothelial character. ×360.

Fig. 11. Section through the decidual tissue, showing a small maternal blood vessel, the endothelial cells of which have become typical giant cells. ×360.

Fig. 12. Section through the placenta at a stage rather earlier than that shown in fig. 25. The character of the giant cell network near the margin of the placenta is clearly indicated. The spaces between the cells are occupied by maternal blood. ×230.

Fig. 13. Section through the fairly late placenta near its margin. The giant cell network has attained its maximum development. ×220.

Fig. 14. Section through a similar region to the preceding one, showing the brown granules around the periphery of the giant cells. ×220.

Fig. 15. Section through the antimesometrial side of the decidual swelling close to the muscularis mucosae. An isolated giant cell measuring ·3 mm. in length is lying amongst the cells of the mucosa. ×150.

Fig. 16. Section through the wall of the implantation cavity, showing the structure of the giant cell network and its intimate connection with Reichert's membrane, on the right. To the left may be seen maternal symplasma formed from the decidual cells under the influence of the giant cells. ×220.

Fig. 17. Section through the wall of the implantation cavity. On the right is Reichert's membrane attached to the inner (right) surface of which are the isolated cells of the parietal yolk-sac entoderm. On the left of the giant cells is the decidual tissue, the portions of which nearest the giant cells are forming a symplasma. ×220.

Fig. 18. Section through the wall of the implantation cavity. On the right is the giant cell network, containing maternal blood, on the left the decidual tissue, which is becoming converted into a symplasma. ×220.

Fig. 19. Section through the wall of the implantation cavity, showing a large giant cell in process of ingulfing maternal symplasma. ×220.

Fig. 20. Section through the implantation cavity wall showing a large giant cell in the cytoplasm of which are masses of maternal symplasma. ×200.

Fig. 21. Longitudinal section through the egg-cylinder of the Field Vole—*Arvicola agrestis*. ×100.

Fig. 22. Section through the yolk-sac splanchnopleur of the late embryo, near its attachment to the placenta. Compare figs. 25 and 27. ×230.

Fig. 23. Section through the placental margin showing the growth in thickness of Reichert's membrane and its intimate connection with the placental giant cells. Embedded in the membrane are maternal leucocytes, while adherent to its inner (upper) surface are the cells of the parietal yolk-sac wall. The spaces between the giant cells are filled with maternal blood. ×380.

Fig. 24. Section through the margin of the late placenta. At the right hand top corner is the outer wall of the uterus with the regenerated uterine epithelium. To the left of the latter is the newly formed uterine lumen, bounded on the inside by the capsularis, which consists of a layer of giant cells in contact with Reichert's membrane, which attains its maximum thickness in this region. Adherent to its inner surface are the cells of the parietal entoderm, while embedded in it are maternal leucocytes. The large cavity shown in the figure is the yolk-sac cavity ×200.

Fig. 25. Transverse section of the uterus containing a fairly late embryo. The section passes through the allantoic stalk and yolk stalk. The reformed uterine lumen is visible at the antimesometrial end. The capsularis is now comparatively thin. ×12.

Fig. 26. The centre of the placental disc of the same specimen. The general character of the placental labyrinth, and its relations to the cellular trophoblast immediately above it, are well shown. ×36.

Fig. 27. The margin of the placental disc of the same specimen, showing the structure of the giant cell network in this region. The membrane limiting the placenta on its lower surface is Reichert's membrane. Attached to the latter are the entodermal cells of the parietal yolk-sac wall. In the lower portion of the figure is the yolk-sac splanchnopleur. The cavity above it is the yolk-sac cavity, that below it is the extra-embryonal coelom. ×36.

ANATOMICAL NOTES ON THE ACCESSORY ORGANS OF THE EYE OF THE HORSE

By Maj.-Gen. Sir FREDERICK SMITH, K.C.M.G., C.B.,
Fellow and Hon. Associate, Royal College of Veterinary Surgeons

	PAGE
Periorbita	366
Muscles of the Eyeball	369
The Fascia of the Globe	375
Capsule of Tenon	377
Nerve Supply to the Muscles of the Eyeball	378
Fat Deposits	382
Membrana Nictitans	385
Lachrymal Apparatus	386
The Eyelids	387

THE PERIORBITA

The orbit of the horse is not a bony cavity; it is little more than a rim of bone, open behind. In this rim the eyeball is lodged, but the muscles are accommodated in the temporal fossa from which they are cut off by being enclosed within a membranous sac known as the *ocular sheath* or *periorbita*.

The periorbita is a cone-shaped fibro-elastic bag extending from the optic hiatus to the margin of the orbit; on its temporal side the sheath is protected by the temporalis muscle, fat, the coronoid process of the lower jaw, and the zygoma; on its nasal side is the thin bony wall of the temporal fossa.

The periorbita arises at the optic hiatus of the sphenoid bone, and passing forward is closely adherent throughout its length to the thin bony wall just mentioned, but its most powerful attachment is to that edge of the orbital process of the frontal bone which looks towards the temporal fossa. To this the whole of the temporal surface of the sheath is secured. After this attachment it continues forward, lines the bony orbit, and reaching the anterior margin splits into two layers; one unites with the periosteum of the face, the other runs into the eyelids and forms the basis of their structure.

Two short ligaments on the temporal surface of the sheath attach it above and below in the neighbourhood of the orbital process, while in the vicinity of the optic hiatus ligamentous material derived from the external pterygoid muscle and a band of fibrous tissue from the sheath of the maxillary division of the fifth nerve form part of its structure.

In general appearance the periorbita is fibrous, the fibres running in several directions, but the majority sweeping backwards from the orbital process. In the region of the process it is distinctly tendinous, and large glistening fibres are present which appear to be intimately connected with the masseter muscle.

Along the middle of the temporal surface is a long broad white strip of tissue which resembles a muscular band of the intestine and runs nearly its whole length. It is not elevated above the surface of the periorbita and is not composed of muscular tissue.

The normal colour of the periorbita is that of fibro-elastic tissue, but a large vein enters its base which discolours this part, especially in the region of the optic hiatus. Further it is difficult to secure specimens entirely free from haemorrhage into the ocular muscles, and this gives a pink colour to the membrane, especially in formalin preparations.

The periorbita consists primarily of an internal and an external layer. The internal is a thin white, and in parts semi-transparent membrane which encloses every part of the eyeball and its appendages. The external membrane, on the contrary, is thick, opaque, and does not cover the whole structure, but mainly its temporal surface. The external layer is composed of tendinous and fibro-elastic material, together with unstriped muscle fibres.

Various statements have been made as to the amount of plain muscle fibre found in the periorbita of animals; in the horse there appears to be but little, but the matter is at present under investigation.

Within the bony orbit, namely that part actually containing the eyeball, the periorbita functions as periosteum. Here it is yellowish in tint. On the inner wall there is a periosteal layer which is quite distinct from the inner thin layer of the periorbita.

The origin of the periorbita is from the dura mater surrounding the structures which enter the orbital hiatus through the various foramina. All the nerves are enveloped in a layer of dura mater which at the foramina opens out and forms the inner layer of the periorbita which extends forwards to the orbital rim. If the various canals leading to the optic hiatus be opened up it is possible to remove the contents and dural sheath intact, and gradually strip the periorbita completely forward to the orbital process. At this point a knife must be employed to divide the attachment of the external layer, which can be done without opening the periorbita by working close to the bone. The whole may now be stripped forward to the orbital rim, where it is again attached but can be separated by the handle of the scalpel when it is found to run into the periosteum of the face. It is possible by the exercise of patience to remove the periorbita entire from hiatus to orbital rim, and thence onwards to the periosteum of the face, in such a way that a complete fibrous cast of the orbit remains, which retains the shape of the bony original. In such a preparation it is impossible, excepting by the presence of the fibrous rim of the orbit, to determine where the periorbita ends and the periosteum of the face begins.

The periorbita on its temporal surface is of great strength and thickness, especially in the region of the orbital process; the nasal wall and a portion of the floor are thin, for here the external tunic is absent. Though cone-shaped in its length, it is flat on its nasal face, and partly concave on its temporal,

in the region of the orbital process, where it has the appearance of being pulled inwards under great tension. This concavity is retained in hardened preparations, but in the fresh periorbita it disappears when the membrane is excised. The most concave area is opposite to the external rectus muscle.

The periorbita is perforated at several points to afford entry to certain structures and exit to others, but the most remarkable perforation is that due to a large vein, known as the alveolar or reflex, entering it from the face. This vein shortly before it penetrates the ocular sheath is a large venous cistern big enough to admit a finger; just before it enters the periorbita it contracts to the size of a lead pencil; this immense vessel boldly enters near the floor close to the optic hiatus where it loses its external coat which is plastered over the surface of the periorbita. It is the blood in this vein which so deeply stains the ocular sheath in the neighbourhood of the hiatus. The vein, however, does not penetrate into the interior of the sheath; it runs between its coats and, receiving the ophthalmic veins in its course, enters the foramen rotundum and so gains the cavernous sinus of the brain. There are no valves in the vessel outside the periorbita, but in the foramen rotundum valves exist and indicate the direction of the stream which is from without inwards, a remarkable anatomical arrangement the necessity for which is by no means clear.

Anticipating what has yet to be said about the origin of the muscles of the eyeball, it is evident, if the above description is clear, that these arise from the inner layer of the periorbita, namely from that layer provided by the dura mater, for when the membrane is stripped from the orbital hiatus and temporal fossa, as described above, all the muscles come away with it. Further, as the entire contents of the orbit may with equal readiness be stripped, leaving within them the loop formed for the passage of the superior oblique muscle, it is evident that this loop is also attached to the periorbita. Finally, in the stripping process the origin of the inferior oblique muscle comes away within the periorbita, so that this muscle likewise obtains its origin from the ocular sheath. We know of no other muscles or tendinous loops in the body of the horse which arise from membrane rather than directly from adjacent bone.

It is obvious that the periorbita forms a membranous socket for the eyeball, but more especially for its accessory organs. The great depth at which it lies is sufficient to ensure its safety; nevertheless there is always a large pad of fat covering the whole of its temporal surface which extends upwards and completely fills the temporal fossa where not otherwise occupied. This pad of fat is of considerable length and thickness, and is so completely moulded into and over the structure that all the surrounding tissues, the great branches of the fifth nerve, the blood vessels, and every crevice and cranny created by the periorbita itself, are filled with fat.

MUSCLES OF THE EYEBALL

All the muscles of the eyeball, including those of the eyelid, arise within the periorbita; even the inferior oblique muscle, the origin of which is so distant from the others, arises within this membrane. The seat of origin is within the optic hiatus, a relatively deep recess formed by the sphenoid bone, bounded on the temporal side by the sharp bony pterygoid crest and on the nasal side by the inner bony wall of the orbit. In this recess there are four foramina, superiorly the ethmoid, giving passage to the ethmoid nerves and vessels, next the optic, giving passage to the optic nerve, below this the foramen lacerum orbitale affording passage to the third, sometimes the fourth, ophthalmic division of the fifth nerve and to the sixth nerve together with certain blood-vessels, and the inferior—the rotundum—through which passes the maxillary division of the fifth nerve and its vessels. The area of the recess which gives origin to the muscles of the eyeball is about 20 mm. in length and 10 mm. in width. Within this small space numerous structures of extraordinary importance are located, including the origin of seven muscles; it is no wonder that the dissection is one of extreme difficulty.

With one exception all the muscles arise from the inner or nasal wall of the optic hiatus; they do not arise from the pterygoid crest. The muscle superiorly situated in the optic hiatus is the superior oblique, immediately below is the levator of the upper lid, then the superior rectus and the internal rectus, next the retractor, finally the external rectus and the inferior rectus. The muscle origins are not in all cases sharply defined, for the reason that some are linked together; for instance the retractor gives origin to the external rectus and is joined to the superior and inferior recti. Most of the muscles have tendinous material in their origins; this is especially true of the retractor and external rectus. Though bony origins have been assigned to the muscles, in reality they do not arise from bone but from periorbita. This may be stripped off the bone as described above, in which case it carries the muscles with it.

At their attachment to the globe all the recti and the superior oblique have a tendinous insertion, but the inferior oblique and the retractor have a wholly muscular insertion.

The longest of the recti muscles is the superior, the shortest are the external and internal; but in the group the longest muscle is the superior oblique, the shortest the inferior oblique, the retractor coming next. Excluding the retractor, the external and internal recti are the thickest and most powerful muscles, while the widest muscle is the external rectus. The retractor at its origin has the most numerous connections with other muscles, viz. the external rectus and the superior and inferior recti.

The *superior rectus* muscle arises below the ridge which separates the optic from the foramen lacerum orbitale and close to the latter, the optic nerve being on its nasal side. It is also attached to the retractor. The muscle, like all the recti, swells out from its origin so that its body is of some substance. As it approaches the globe it detaches from its surface a fascial covering and

immediately afterwards a second and inner fascial sheet which envelopes the muscle and forms a bursa through which it passes. The external fascial covering is a firm moderately thick layer of yellow fascia, which on reaching the globe joins up with similar fascial coverings from the neighbouring muscles. The fusion of the fascial coverings forms a "belt" around the equator of the globe, the arrangement and subsequent distribution of which has to be studied in the section devoted to the fascia of the eye. The inner layer of fascia which forms a bursa through which the muscle moves is described in the section on fascia. Its importance here is its function in keeping the recti muscles in position on a globular surface. On opening the bursa it is found to be moist and shining; the muscle lies in a distinct furrow formed in the underlying fat; though the bursa in front is open it is cut off behind. The muscle cannot be lifted out of the groove until a delicate connective tissue attachment is divided, which shows the amount of play to be very limited, as indeed would be expected. Having passed under the lachrymal gland the superior rectus ends in a flat, wide and thin tendon which spreads itself out in order to obtain a wide area of attachment to the sclerotic. The width of the tendon is about 25 mm. but the area of attachment is larger than this by the tendon fusing with the deep layer of fascia. The tendon is inserted into the sclerotic somewhat obliquely so that on its temporal edge it is 5 mm. from the corneo-scleral junction, while on the nasal edge it is 7 mm.

The branch of the third nerve supplying this muscle enters on the temporal surface close to its origin and, breaking up into four or five fibres, spreads out in its interior.

The *inferior rectus* muscle arises from the nasal wall of the orbital hiatus in front of the foramen lacerum orbitale; it is also attached to the inferior part of the retractor. It at once separates from this muscle and in its passage towards the globe travels the whole distance in contact with the external rectus, being in this respect exceptional, as the recti muscles mostly diverge. On the floor of the orbit it runs side by side with the lower border of the cartilago nictitans and, passing between the inferior oblique muscle and the globe, terminates in a tendon which is inserted into the sclerotic. The tendon is the smallest of the recti group, measuring only 17 mm. in width; it is set on somewhat obliquely, so that its temporal edge is 8 mm. and its nasal edge 10 mm. from the corneo-scleral rim.

The inferior rectus on approaching the globe gives off the usual two layers of fascia, an outer and an inner. The former runs to the "belt"; the inner forms a bursa for the muscle. The bursa is located in a pad of fat and lies at some depth, the fat being channelled for the passage of the muscle. The inner layer also embraces the inferior oblique muscle where the inferior rectus passes between it and the globe, and this enables the inferior oblique to be kept in its place on the globe of the eye. The fascia is also inserted into a crescent-shaped membrane, composed of periorbita and periosteum, on which the lower eyelid is built.

On the upper surface of this muscle, close to its origin, is the ophthalmic ganglion, in the region of which a nest of nerves is found in the substance of the muscle. Coursing its way obliquely over the body of the muscle is a long branch of nerve which passes its outer edge and eventually turns under its lower surface. This nerve supplies the inferior oblique muscle[1].

The origin of the *external rectus* muscle is peculiar; it arises from the temporal surface of the retractor, a little below its highest point and above the inferior rectus. It immediately leaves the retractor and pursues its way to the globe, the lower edge of the muscle being for the whole distance in contact with the inferior rectus. The muscle is wide and powerful, being in fact the widest of the recti group. On approaching the globe it gives off first an outer, and then an inner, layer of fascia, the outer as usual forming a part of the "belt." This outer sheath is very large owing to the width of the muscle; the inner, or bursal sheath, is present but the groove through which the muscle passes is shallow. This muscle is inserted into the sclerotic by a wide tendon which is attached to the globe above the insertion of the inferior oblique muscle, close to the outer canthus of the eye. The end of the tendon is vertically placed, its superior border being 14 mm. from the corneo-scleral junction, and its inferior border 3 mm. distant. So close indeed is this tendon to the cornea that a portion may be found under the pigmented conjunctiva found at the outer canthus.

The *internal rectus* arises from the nasal side of the orbital hiatus, below and in front of the ethmoid foramen. This muscle prior to insertion furnishes the usual double layer of fascia and provides itself with a bursa deeply buried in a fat deposit. Its insertion into the sclerotic occurs far back from the corneo-scleral junction, the explanation being that it has to make way for the cartilago nictitans; there is no tendon of the recti group inserted so far back. The upper edge of the tendon may measure 20 mm. from the corneal rim, the lower edge 15 mm.

The fascial bands from this muscle are important[2]; the outer sheath is distributed to the nasal aspect of the levator of the lid, and keeps the nasal side of the lid applied to the globe; it also runs to the upper edge and nasal surface of the invisible or deep-seated portion of the cartilago nictitans, and keeps the cartilage bound down to the eyeball. A portion runs forward to the conjunctiva covering the visible part of the cartilago in the conjunctival sac, to the upper edge of which it is attached, and this keeps it applied to the eyeball. There is also a firm attachment of this sheath to the rim of the orbit, in front of and above the lachrymal sac where the upper and lower eyelids meet in the lachrymal pool. This attachment assists to keep the tissues of the "corner of the eye," including the caruncula, in place. The inner fascial sheath also furnishes a band to the deep-seated portion of the cartilago, b[illegible]

[1] No name has been assigned it by anatomists.

[2] Owing to their importance they are dealt with here in detail, and referred to generally in [illegible] section dealing with the fascia.

to its upper edge and temporal surface, namely the surface applied to the eyeball; it is further connected through the conjunctiva with the visible portion of the cartilago, and terminates beneath the conjunctiva at the corneo-scleral junction.

The *superior oblique* muscle is the longest in the orbit; it is also very narrow. It arises close to and behind the ethmoid foramen. It is the most superiorly placed muscle in the optic hiatus, being above the level of the optic nerve and on the nasal side of it. In its course towards the eyeball the superior rectus is on its temporal margin, and on its nasal side and below is the internal rectus.

Having reached the globe the muscle enters a fibrous canal, formed of periorbita, which curves upwards; this directs the muscle away from the internal rectus. At the end of the canal is a loop, also formed of periorbita. As the muscle passes through the loop its direction is profoundly altered, for it now travels almost at right angles to its original course and in this way, by passing beneath the superior rectus, it travels across the globe and reaches the temporal side of the eyeball. The superior oblique is the only muscle of the eyeball to which the periorbita is connected, and the only part of the globe of the eye to which the periorbita is attached is the fibrous canal above described. The extraordinary change in direction taken by the superior oblique must be considered more closely.

The periorbita sends a reflection under the superior oblique and so isolates this muscle in a canal; this canal is secured throughout its length above to the frontal bone, while below it is attached to the "belt" of the eyeball and neighbouring fat by means of fascia; this occurs in the region lying between the rectus superior and the rectus internus. Within and towards the end of the canal is a loop attached in two places to the frontal bone; the loop is composed of periorbita, and its lumen looks obliquely to the front, namely, towards the orbital opening. The posterior arm of the loop has lying on it a disc of cartilage concave inferiorly; this disc has a gutter on its superior face in which the muscle rests, while on its inferior face is a bursa between it and the posterior limb of the loop. Where the muscle rests on the disc it is narrow, very smooth, and comes to an edge in order to fit into the gutter of the disc. One would expect on slitting up the canal to be able to lift up the muscle out of its bed, but this is not so; though the canal is smooth and glistening the muscle is tacked down to it throughout its length by connective tissue. The muscle terminates in a tendon the insertion of which looks towards the temple and not towards the cornea. The anterior edge of the tendon is 10 mm. from the cornea, the posterior edge 20 mm. from it. As usual the tendon is much wider than the muscle.

The loop is described above as attached to the frontal bone. Strictly speaking this is not correct, for the periorbita of the eyeball encloses the loop which may be pulled away from the bone without much effort; when the periorbita is stripped off, the loop is found intact within. In other words the loop is attached to the periorbita in the same way that the ocular muscles

are attached to it in the orbital hiatus. One is struck with the resemblance of the loop and canal of the superior oblique to the fascial bands and bursa of the recti muscles.

The fourth nerve which supplies this muscle is very small and runs for a short distance along its upper border. When about half way to the eyeball it suddenly bends, its fibres separate and dip into the substance of the muscle.

The *inferior oblique* muscle is the shortest of the series, and it is further distinguished by being muscular throughout, both at its origin and insertion. It arises from a depression close to the edge of the orbit immediately posterior to the lachrymal sac, but its origin is from the periorbita, for if this be detached from the bone the muscle comes away with it. It has the largest area of origin of any of the muscles of the eyeball; this area is somewhat oval or triangular, measuring 12 mm. at its widest part. Its insertion measures 23 mm. or more across. This short, thick and powerful muscle increases in width from origin to insertion; its fibres are curved, the direction of the muscle being from the nasal to the temporal side of the orbit. In its passage from one side to the other it covers the tendon of the inferior rectus. It never loses contact with the globe, and is attached to the sclerotic below the insertion of the external rectus. Some of the fibres of this muscle are continued up the globe and may be found beneath the tendon of the external rectus. Its anterior fibres are placed so far forward as almost to touch the corneo-scleral junction at the outer canthus. At its origin the inferior oblique obtains from the internal rectus a layer of fascia which completely embraces it and so tends to keep the muscle well back in its place. At this point also it is closely applied to the nasal surface of the cartilago nictitans and so keeps this in contact with the globe. The nerve supplying this muscle takes, as previously indicated, a very roundabout course. It is a relatively large flat nerve in which the strands can distinctly be seen; it enters the muscle close to its origin and at once breaks up into a nest of fibres.

The *retractor* muscle has a singular origin. Within the canal of the foramen lacerum orbitale may be found[1] two small muscles with fine tendons; one is 25 mm. in length, the other 6 mm. These two tendons arise from the sheath surrounding the nerves, and the delicate muscles on gaining the periorbita at once join the retractor into which they are incorporated. The retractor has its chief origin from the nasal wall of the hiatus just below the small bony ridge which separates the optic from the foramen lacerum, and in front of the latter. It gives origin to the rectus externus and is attached to the recti superior and inferior. Into the origin of the retractor a considerable amount of tendinous material enters. The optic nerve is above the retractor in the hiatus but a few millimetres further forward the muscle is in contact with the nerve, embracing its temporal and inferior surface, and a little later the whole nerve is enveloped, lying practically in the centre of the muscle. The general shape of the muscle is that of a cone, the base of which is applied to

[1] Their absence has been observed.

the eyeball and contains a core of fat; the fibres of the muscle are loosely connected so that the bundles of muscle tissue are readily seen, and fibres, some as delicate as sewing cotton, can be obtained without difficulty. The capsule of Tenon envelopes the general structure and also sends in septa, the larger of which have the effect of grouping the muscle into four quarters corresponding to the recti series. The retractor is inserted into the sclerotic over a wide area, but the insertion on the temporal side of the globe is wider than on the nasal; some of these fibres run so far forward as to be inserted above the inferior oblique muscle. Speaking generally the muscle is inserted into the posterior half of the globe, and it is perhaps the sinuous outline of the insertion more than anything else which indicates that it is roughly arranged in four groups. On its nasal and lower surface the retractor muscle is concave in hardened preparations to accommodate a large pad of fat located there; on its temporal side the muscle is also concave in order to accommodate the external rectus. The superior group of fibres is convex, and over these is moulded the superior rectus muscle. The retractor is completely hidden from view until the recti and superior oblique muscles have been removed.

The relationship of the origin of the retractor muscle to the optic nerve has been mentioned above: 10 mm. in front of the hiatus it completely surrounds the nerve which lies in its centre. The nerve is not in direct contact with the muscle, as it is contained in a large, white, loose fibrous sheath. This sheath is derived from the dura mater and from its surface minute threads of muscle may be seen arising and joining the general body of the retractor[1]. The nerve does not penetrate the central part of the sclerotic but dips down and enters the eyeball near to the floor. When the retractor muscle reaches the globe it spreads out to obtain attachment to the sclerotic, and the large space thus created in the middle of the muscle is filled up with fat.

There is no branch of the third nerve to the retractor; it is supplied by the sixth, which enters it by a relatively small branch close to the head of the muscle. Speaking generally the retractor is singularly free from nerve fibres; in this respect owing to its size it presents a marked contrast to the other muscles of the eyeball.

The remaining muscle from the optic hiatus is the *levator* of the upper lid. It arises by a somewhat tendinous attachment immediately above the optic foramen. This small muscle in its passage forwards lies adjacent to and on the nasal side of the superior rectus. When it reaches the lachrymal gland it passes beneath it, becoming wide and fan-shaped, the fibres swerving towards the temporal side of the lid. Through the medium of the outer layer of fascia the tendon is spread over the eyeball from the inner to the outer canthus.

Though the muscles moving the globe of the eye originate in a bunch, as it were, they rapidly diverge in order to reach their destinations. The inferior and external recti, however, lie side by side until they reach the globe; the

[1] The reason of this is not clear; the fibres are mere threads though of remarkable length, and each is furnished with a minute glistening tendon.

superior rectus and superior oblique are also close together; while the inferior and internal recti lie widely apart. When the contents of the orbital cavity, i.e. the globe and its muscles with their periorbital cover, are viewed in position from above and behind, they resemble a pear in shape.

Relative to the corneo-scleral margin the external rectus occupies the largest space and is the nearest to the cornea; furthest away is the internal rectus; the superior and inferior recti occupy a midway position. Of the oblique muscles the insertion of the anterior fibres of the inferior is as close to the cornea as that of those of the external rectus, but the superior oblique is placed some distance back, its anterior fibres lying just behind the superior rectus. In connection with the insertion of the recti tendons their fascial connections cause their attachment to the globe to be much wider than is actually represented by the tendons themselves. Nor are the insertions of any of the muscles truly vertical or horizontal; they are all more or less on the curve, the inferior rectus being somewhat obliquely placed as its tendon lies between the inferior oblique muscle and the globe. Both oblique muscles have an oblique insertion.

THE FASCIA OF THE GLOBE

The fascia of the globe is complex in its arrangement. Roughly speaking there are two layers of fascia, an outer and an inner, and both of these are derived from the recti muscles. As previously pointed out, all four recti, just as they approach the globe, give off a fascial sheath, and if this be opened a second fascial sheath, also given off by the muscles, may be seen within. The outer sheaths of the four recti coalesce and thereby form a sheet of fascia over the globe, especially well marked by its colour and thickness at the equator, where it constitutes a "band" or "belt"; similarly all the inner sheaths coalesce and form a fascial sheet distributed to many parts of the eye anterior to the equator. These features must be dealt with in detail.

The outer fascial sheath comes off from the muscles as a thin transparent membrane which, by the time it reaches the globe, is yellow, elastic, thick and strong. Around the equator of the globe it forms a "belt" due to the fact that the sheath provided by each rectus, very shortly after its formation, fuses with that of its neighbour, producing a uniform membrane. The sheath when formed is not adherent, excepting for some very delicate connective tissue, to the muscles within, and it may readily be picked up with forceps from their surface. The "belt" is formed as explained above. Running forward past the equator the membrane of the "belt" changes in character, becoming fine, thin and semi-transparent, and in this form it runs from all meridians to the corneo-scleral junction for insertion.

The inner fascial layer—also from the recti muscles—arises at a point nearer to the globe than the outer layer; it is elastic, much finer in quality than the outer, and more translucent. It comports itself differently from the outer layer, as it forms a separate sheath for each rectus at the equator;

the sheath is shining, showing that some fluid exists to prevent friction. Having formed the sheath it coalesces with its neighbours and spreads out as a vast sheet which encircles the globe anterior to the equator. This sheet is external to the insertion of the recti tendons, is loosely tacked down to the sclerotic by a fine connective tissue, and finally ends at the corneo-scleral junction.

The inner and outer layers of fascia thus form two vast spaces, one between the outer and inner layers and one between the inner layer and the sclerotic (but external to the recti tendons). The retractor muscle possesses no fascial sheath, that of the inferior oblique is derived from the internal rectus and external fascial layer of the globe, but the superior oblique possesses a very extensive sheath. It, however, is provided not by the muscle itself, as in the case of the recti, but by the periorbita, and forms the fibrous channel and loop already described, through which this muscle passes, while at the same time it plasters it down to the globe.

One important use of the inner fascial layer is to provide a bursa through which each of the recti plays, not that the movement is considerable, for the muscle is lightly tacked down in its channel by means of connective tissue; in addition it keeps each muscle in position on the globe, as is evident from the depth of the furrow through which the muscle passes. This depth is obtained by a mound or eminence of fat flanking either side of the bursa; this is especially well marked in the case of the superior rectus where the structure, when laid open, strikingly resembles the flexor tendons where they pass over the sesamoids at the fetlock joint. The external rectus, being a very wide muscle and therefore suited to keep in its place on the convex eyeball, has only a shallow furrow, though the bursa and sheath are well marked. The rectus inferior and rectus internus have very deep furrows, these being provided by the pad of fat through which each muscle passes to reach the eyeball. While the bursal arrangement for the muscles is formed by the inner fascial layer, the outer fascial layer plays the same part as the annular ligament of a joint and keeps the muscles in their furrows.

In addition to these important functions, the two layers of fascia, when they subsequently spread out as independent annular membranes towards the cornea, have other anatomical functions to perform.

The external layer joins the tendon of the levator of the upper lid and thereby renders it much wider so that it is able to operate from the inner to the outer canthus. It furnishes bands of ligamentous material to the deep portion of the cartilago nictitans and so keeps the cartilage closely applied to the globe; it provides a layer which runs into the substance of both upper and lower lids; it furnishes attachment to the deep portion of the conjunctiva of the eyeball and also to the special fold of conjunctiva which envelopes the visible cartilago nictitans; it supplies a band which helps to secure the junction of the upper and lower lids at the inner canthus to the rim of the orbit and so keeps the lachrymal pool in position; on the floor of the eyeball it forms a complete sheath for the inferior oblique muscle, in fact envelopes it and so

keeps it back in its place on the globe; and finally, unlike the layer in the upper eyelid, it obtains attachment to the crescent of periorbita on which the lower lid is moulded.

The internal layer of fascia is attached at its origin to the outer layer of fascia and also to the fat prominences and pads between the recti muscles; it is concerned in keeping the cartilago in position on the globe, and by its connection with the tendons of the recti muscles it increases the area of their attachment; it is also attached to the conjunctiva, especially that part of it connected with the visible portion of the cartilago; a portion of it runs into the lower lid, while the main sheet terminates in the same way as the external layer by attachment to the entire corneo-scleral margin.

The fascial connections furnished by the internal rectus are more elaborate than those of the other recti and have been specially dealt with in the description of this muscle.

Between the origin and insertion of the inner and outer layers of fascia there are structures intimately related to them other than those already mentioned; especially is this true of the masses of fat which envelope the globe. These receive a cover from both layers which is specially intended not only to invest but also to penetrate the mass or deposit in all directions, so that the fat of the eyeball is rendered quite fibrous, a point which is insisted upon in the section devoted to fat deposits.

CAPSULE OF TENON

A thin diaphanous membrane is found within the orbital sheath. It resembles the mesentery in fineness and transparency, and the resemblance is increased by the presence of streaks of fat in its substance. This membrane extends from the optic hiatus to the eyeball. It is reflected inwards in such a way that every muscle receives a sheath of this substance which can be readily picked up by forceps from its surface; between the muscles the septa enclose such fat, vessels, or nerves as may be in their vicinity. From this it is evident that a complicated arrangement exists whereby every muscle is enclosed in a capsule, the capsules of neighbouring muscles meeting at the septa. The structure is known as the capsule of Tenon. So thin is this capsule that its presence in places is difficult to determine unless it be lifted up or punctured, when air bubbles run beneath it and prove its presence. The precise method by which the capsule terminates on the globe of the eye is not clear. It is generally accepted that the capsule of Tenon is connected with the lymphatic system, but we have no information as the result of our dissections. The capsule of Tenon is quite distinct from the fascial sheaths of the recti muscles.

NERVE SUPPLY TO THE MUSCLES OF THE EYEBALL

The nerves to the muscles of the eyeball are supplied by the third, fourth, fifth and sixth cranial nerves, the arrangement being complex. Two distinct branches of the fifth are engaged, namely the ophthalmic and superior maxillary divisions; the former enters the periorbita direct; the latter has to penetrate it from without. The nerve supply is sensory, motor and secretory; both branches of the fifth nerve are sensory, the third, fourth and sixth are motor. The secretory nerves are contained in the fifth and sympathetic.

The sensory nerves, with one exception, lie on the surface of the muscles and are at once seen on slitting up the periorbita. They are large flat branches entangled in fat and capsule of Tenon, and may readily be divided into three groups. The superiorly placed nerve is the *frontal*. It is derived from the ophthalmic division of the fifth and enters the periorbita at the optic hiatus immediately on the temporal side of the superior rectus muscle close to its origin. It at once turns upwards, crossing obliquely the superior rectus and levator muscle as it travels from the temporal to the nasal side; when on the levator muscle and following its direction, it suddenly penetrates the inner layer of the periorbita. It then runs in a membranous canal, formed by two layers of periorbita, for a distance of about 40 mm. and finally emerges outside the ocular sheath in the region of the orbital process, and so reaches the supra-orbital foramen through which it passes and is distributed to the tissues of the forehead and upper eyelid. The group of nerves below the frontal is the *lachrymal*. These are also derived from the ophthalmic branch of the fifth. The main trunk emerges from the temporal side of the optic hiatus over the junction of the superior and external recti. As it pursues its way over the surface of the muscles to the lachrymal gland it forms two or three branches; the upper one or two as the case may be enter the lachrymal gland at its posterior border and break up into several branches which are lost in its substance. Quite large branches may be traced forward for some distance in the gland. The lowermost nerve of this group has no connection with the lachrymal gland. Having reached a point corresponding to the zygoma, it turns upward, penetrates the periorbita and so reaches the orbital fossa; keeping close to the zygoma it is eventually distributed to the temporal region. It ought to be designated the *temporal* nerve. This nerve, while still within the periorbita, may receive, midway between the optic hiatus and the globe, a branch from the inferior maxillary division of the fifth. The lowermost group of nerves, designated the *zygomatic*, is derived from the maxillary division of the fifth, which is outside the periorbita. They run forward to this structure and penetrate the outer tunic, running between the coats as far forward as where the alveolar or reflex vein enters; at this point they complete their penetration of the periorbita and are found lying just above the fissure between the external and inferior recti; on approaching the globe they divide into two or more branches which eventually supply the tissues at the outer

canthus; some fibres then pass through the fascia of the inferior rectus muscle and thence through that portion of the periorbita on which the lower lid is built and are finally distributed to the lower lid.

There is a connecting nerve between the middle and inferior groups; sometimes, and perhaps more generally, it runs from the maxillary to the ophthalmic division, but the converse has been observed. In this case the connecting branch, a fine thread of nerve, took an unusual course. Running in the fissure between the superior and external recti, it got beneath the external rectus, then running on the upper surface of the retractor in the direction of the temporal side of the eyeball, it finally pierced the external rectus and joined the inferior group close to the eyeball.

All the above branches of the fifth are remarkable for their size, which they retain up to the tissues they supply; they are all flat nerves in which the bundles are distinctly seen; they all run on the surface of the muscles, and all the branches described are seen from the temporal side of the orbit. There are only two branches of the fifth on the nasal side, and these are contained in the next group of nerves to be described.

When the superficial group of nerves has been removed, the deep-seated are brought into view, though it is necessary first to clear away some capsule of Tenon and fat. It will be observed that with one exception all the nerves now to be described appear to be very short, the explanation being that they have scarcely shown themselves at the optic hiatus before they dip into and between the various muscles of the eyeball and are consequently lost to view. Viewed as they lie in position they present the following general arrangement:

The uppermost nerve is the fourth. It is also the finest and can readily be traced some distance upwards before it disappears over the levator muscle in order to gain the superior oblique. The nerve below the fourth is the third; it will be found lying on the temporal surface of the superior rectus muscle and is almost at once lost to view. Immediately below the third is the fifth (ophthalmic division) which will be found lying between the origins of the superior and external recti. In the same furrow is a small branch of nerve, the sixth, which is covered by some connective tissue and a blood-vessel; it almost immediately dips between the muscles and disappears. All these nerves enter the periorbita by the canal leading to the foramen lacerum orbitale, though sometimes, and in the writer's experience more commonly, the fourth enters by a separate canal. On laying open the foramen lacerum orbitale the remarkable thickness of the sheath investing these nerves is very evident. Until the mass is lifted from the canal only one nerve can be seen. This is the ophthalmic branch of the fifth within which is contained the third and sixth, the fifth either being rolled around them, or fitting into an angle formed by the third and sixth nerves. The ophthalmic branch is the largest; its bundles of nerve fibres are quite evident, and the nerve is moreover flat; the third, fourth and sixth nerves are round.

On entering the optic hiatus the strong investing sheath of the nerves,

which is also the membrane lining the canal, at once leaves the nerves and spreads out to form the periorbita. In this process it fuses with the sheath investing the optic nerve, for both sheaths take part in the formation of the periorbita.

Fifth nerve, ophthalmic division (inter-muscular branches). The distribution of the frontal, lachrymal and zygomatic branches of the fifth nerve has already been traced; it will be remembered that they are all extra-muscular. The remaining portion of the fifth which has to be dealt with is the inter-muscular branch.

The nerve on issuing from the optic hiatus lies in the fissure between the superior and external recti. Some fibres of the latter muscle may be split to allow of its passage to its position beneath the superior rectus. Here it is resting on the retractor, crossing this muscle obliquely towards the nasal side, but it has only proceeded a few millimetres when it divides into two branches, one continuing forwards to the nasal side, the other and posterior branch running to the nasal side only as far as the superior oblique muscle and then turning backwards. The branch of nerve running forward is the inferior trochlear, the one running backwards is the ethmoidal. There is a great difference in the appearance of these two nerves. The ethmoidal maintains the flattened character and well-marked bundles of fibres seen in the parent trunk; the inferior trochlear is round and does not exhibit any bundles to ordinary observation. Throughout its course up to the point of division the main trunk is accompanied by the ophthalmic artery which at first lies in front of and then behind the nerve. In order to show the above features the superior rectus must be divided and turned back.

The *ethmoidal nerve*. Shortly after the bifurcation of the main branch this nerve makes a sharp bend backwards and inwards, so as to lie under the superior oblique muscle; from here it travels backwards on the top of the internal rectus into the optic hiatus lying on the nasal side of the optic nerve; it then bends sharply at right angles and passes out of the orbit through a small foramen and re-enters the cranial cavity in the vicinity of the olfactory bulb; it at once sharply bends forward, keeping close to the bone, and enters the ethmoid cells. Before escaping by the foramen into the olfactory region it gives off a long fine branch of nerve which travels on the nasal side of the internal rectus and terminates in the lateral fat pad on the inner side of the globe. This branch has no name. It is by no means clear why the ethmoid nerve requires so confusing an arrangement; as we have seen, it is a nerve intended for the organ of smell and not that of sight, yet it enters the periorbita, dives between the muscles of the eyeball, makes two sharp bends and escapes from the periorbita into the cranium, then leaves the cranium and enters the ethmoid cells.

The *infra-trochlear* branch runs obliquely forward on the retractor muscle towards its nasal edge, and passes between the superior oblique and the internal rectus; remaining in contact with the last named muscle, and hidden

from view, the nerve passes under the bend of the superior oblique through the lateral fat pad which plasters over the terminal portion of the internal rectus, and so gains the nasal side of this muscle; running straight forward it pierces the periorbita in the region of the internal canthus and escapes from the orbit by means of one or two foramina in the orbital rim just above the lachrymal sac. During its course it furnishes sensation to the cartilago nictitans, lachrymal sac and neighbouring structures, and finally to the tissues situated at the inner canthus. It is difficult to understand why this nerve was not placed with the other sensory nerves on the surface of the muscles instead of being deep-seated between them. It corresponds to the long nerve on the temporal side, the zygomatic, which supplies the external canthus and lower lid.

The following nerves are purely motor:

The *third nerve* in contrast to the fifth is round and its bundles of fibres cannot be distinguished by the naked eye. While in the canal before reaching the foramen lacerum orbitale it divides into two branches, a long and a short, which remain side by side, the short being superiorly placed. On leaving the optic hiatus the nerve lies between the superior and external recti, and the short branch at once enters the origin of the superior rectus, penetrating the muscle on its temporal side and breaking up into fibrils. The long branch cannot be seen from the surface as it lies immediately beneath the short, but it turns down and, passing between a few fibres of the superior rectus, reaches the retractor a few millimetres behind the point where the fifth nerve bifurcates. The nerve now runs still more deeply, piercing the retractor close to the optic nerve on its temporal side and being attached to its sheath. It then gets below the optic nerve in order to form the *ciliary* or *ophthalmic ganglion*. The ganglion lies on the inferior rectus muscle or alternatively on the fissure between the inferior and internal recti, and is situated immediately beneath the optic nerve. The ganglion is small and occurs on the nerve about 12 mm. from the optic hiatus. Issuing from it are several short stumpy branches of nerve resembling fingers on a hand, which almost at once enter the inferior rectus muscle and break up within its substance into a veritable network of fibres which can be traced forward in the muscle for a considerable distance. From the front of the ganglion is also given off a somewhat longer, though still thick and stumpy branch, which, crossing to the nasal side, almost at once penetrates the neighbouring internal rectus muscle, where it breaks up in its substance into a nest of fibres. No muscles of the eyeball are so richly furnished with nerves as the inferior and internal recti. Another branch runs from the ganglion into the loose outer sheath of the optic nerve. It is very difficult to trace owing to fat, but several fine threads may be seen running within the sheath to the eyeball, where they penetrate the sclerotic and eventually reach the iris and the ciliary body. These are the ciliary nerves.

Inferior oblique nerve. From the anterior part of the ciliary ganglion is given off a fourth nerve, a long well-marked branch which crosses the inferior rectus obliquely towards its temporal side; it now appears on the external surface

of this muscle by passing beneath the external rectus. It runs forward towards the eyeball, lying on the temporal side of the inferior rectus, but gradually gets beneath the muscle, and when opposite to the body of the inferior oblique it bends towards the nasal side and running parallel to the inferior oblique for about 15 or 17 mm. bends sharply to the front, pierces the fascia of the inferior oblique and enters this muscle at its posterior border about 12 mm. from its origin. Just as the nerve enters the muscle it flattens out, thus showing its fibres distinctly, nests of which are formed in the substance of the muscle. No name has been assigned by anatomists to this nerve, so I have called it the *inferior oblique*. Its erratic course is necessitated by the distance the inferior oblique muscle lies from the optic hiatus; this nerve is consequently one of the longest in the orbit.

The *fourth nerve* is very simple; it is a small round nerve contained either in the canal of the foramen lacerum orbitale and so enveloped by the ophthalmic division of the fifth, or else entering the periorbita by a foramen of its own. Within the periorbita it is located above the third, fifth and sixth nerves. Crossing the superior rectus and levator towards the nasal side, it reaches the superior oblique muscle; it runs forward along the upper border of this muscle for a distance of about 30 mm. from the hiatus, and then quite suddenly dips down and penetrates the muscle.

The *sixth nerve* is inferiorly placed in the periorbita, and also in the canal of the foramen lacerum orbitale, where, as already described, it is enveloped by the ophthalmic division of the fifth nerve. While still in the canal it divides into two short branches; on entering the periorbita these cross the external rectus obliquely and penetrate inwards between the origins of the superior and external recti; the small branch proceeds to the origin of the retractor and immediately enters it; the larger branch, which is inferiorly placed, at once enters the external rectus muscle on its inner face. Thus the sixth nerve supplies not only the abductor muscle of the eyeball but also the retractor. In view of its size it is very remarkable that the retractor has only one small motor nerve entering it; this is in great contrast to the inferior and internal recti, both much smaller muscles, which possess a nest of nerve ramifications.

No special branch of nerve has been traced to the levator of the lid.

FAT DEPOSITS

The deposits of fat both between and outside the muscles of the eyeball are complex in arrangement. Fat is found everywhere, both in deposits and layers; indeed, wherever there is a cleft, nook or cranny, whether outside the periorbita or within, there fat will be found. A superficial inspection suggests that the fat deposits are on the nasal side of the globe low down, and on the upper surface of the globe under the superior rectus muscle, with a further deposit on the rim of the orbit corresponding to the lower lid. Dissection, however, reveals that these are not separate fat deposits but one continuous layer, which by the way it enfolds, overlaps and underruns the structures,

appears to have neither beginning nor end. In places the layer is enormously thick, forming veritable pads; this is especially the case where a large space has to be filled in, but the edges of this mass thin out, pass under or around neighbouring muscles, and, having got clear of them, again swell out when the next large space has to be filled in. Whether it is in the space enclosed by the retractor muscle, i.e. in the very heart of the muscles surrounding the globe, or whether it is a thin streak showing itself on the surface between two muscles or a deposit whose measurements are in centimetres, the fat all belongs to one piece or roll. The fat of the orbit is unlike ordinary fat in one essential. It is encapsuled and intersected by fascia so that it is quite fibrous and remarkably tough. In parts, especially around the "belt," the most diligent application of scalpel and forceps fails to clear the surface. In this respect the large masses are much more manageable. A lateral fat pad lies on the nasal side of the orbital contents; as viewed from the surface it is a prominent triangular shaped body, lying in the big space between the internal and inferior recti. The apex of the triangle, which is not sharp but rounded, looks towards the optic hiatus, and reaches within 20 mm. of it. The base extends as far forward as the lachrymal sac and origin of the inferior oblique muscle. This pad runs deeply under and within the inferior and internal recti and comes into contact with the retractor which is rendered concave for its reception; it is deeply grooved for the accommodation of the inferior and internal recti. While the internal rectus passes through the mass, further forward the inferior rectus, towards its insertion, passes outside of the pad. It is at this place, the two muscles being wide apart, that the lateral fat pad is attached to the nasal surface of the cartilago nictitans.

Tracing the course of the lateral fat pad up the globe, and starting at the point where it is penetrated by the internal rectus, we notice that the fat passes upwards under the bent portion of the superior oblique[1] and is here channelled for the passage of the frontal nerve; beneath the superior oblique it forms a prominence, on a part of which the cartilaginous disc of the loop of the superior oblique rests; the remaining portion shows as a pyramidal body of fat between the superior oblique and the superior rectus. This pyramidal mass runs between the levator muscle of the upper eyelid and the superior rectus; under the superior rectus it forms a thick pad of fat which rests partly on the retractor muscle and partly on the upper edge of the internal rectus. This thick mass is the superior pad, which, though given a specific designation, is merely an extension of the lateral pad described above. Like the lateral mass the superior pad is pyramidal, the apex reaching as far back as 30 mm. from the optic hiatus. The deep part of the base ends at the sclerotic under the insertion of the superior oblique, while the superficial part of it is a thin layer which runs over the superior oblique and is confounded with the fascia which ends in the conjunctiva of the globe. Continuing the wanderings of

[1] The expression "bent" indicates the shape of the superior oblique where it enters the fibrous canal, and does not refer to the right-angled turn it makes by passing through the loop.

the superior pad, it passes from beneath the superior rectus to beneath the external rectus, forming the fat prominence, so evident in the region of the "belt" which exists in the division between these two muscles. Some of the fat passes over the outer surface of the externus, though beneath its fascia, but the larger portion is under or within the externus, between it and the retractor muscle, and forms a big prominence at the "belt" between the external and inferior recti; within the inferior rectus this thins down and links up with the big lateral pad on the inner aspect. In this way we have followed the complete encirclement of the muscle of the globe with a continuous layer of fat, thin in some places, enormously developed in others. It has been seen that the large lateral mass is attached to the cartilago nictitans, of which an account will be given in connection with that structure, but nothing has yet been said of the connection of the enveloping mass with that found on the floor of the orbit in the region of the lower lid, nor of the deposit contained within the retractor.

The fat within the retractor is continuous with the superior fat pad through a division in the retractor that lies opposite to the external rectus. The pad within the retractor is pyramidal in shape, the base being applied to the sclerotic. The fat on the floor of the orbit is derived from that portion of the lateral pad which extends to the lachrymal sac. From here in an upward direction a layer of fat extends up the nasal side of the globe as far as the nasal side of the lachrymal gland. The portion which crosses the floor of the orbit from the lachrymal sac runs towards the temporal side where it lies beneath the fascia proceeding to the lower lid. It is a wedge-shaped piece of fat, being thin under the globe and thick towards the eyelid, especially thick, 5 or 6 mm., at that part corresponding to the central point of the lower lid. This fat is particularly fibrous towards the lid; fibrous material, derived from the periorbita and periosteal tissue (on which the lower lid is moulded), enters the fat and so keeps it in position. Moreover, the combined periorbita and periosteum meet the fascia proceeding to the lower lid and so enclose the fat in a fibrous case. The fat from the floor of the orbit then ascends the temporal side of the globe and terminates at the temporal end of the lachrymal gland. The nerves supplying the outer canthus and lower lid penetrate the fat and pierce the periorbita in order to reach the outside tissues. No fat covers the lachrymal gland.

The large venous plexuses of the eye and orbit are in intimate relation with the areas containing fat, especially the partial ring of fat just described as extending from the nasal side of the lachrymal gland beneath the eyeball to the temporal side of the gland.

The deposit of fat outside the periorbita consists of one long roll several centimetres in length extending from the maxillary tuberosity over the whole of the periorbita, and ascending in the temporal fossa until level with the upper edge of the orbital process. It is thick and permeated by a connective tissue which renders it very fibrous. It fills in every space or nook around the periorbita, and covers all the vast nerves and vessels in its neighbourhood.

MEMBRANA NICTITANS

The third eyelid is placed at the inner canthus of the eye; it consists of a deep-seated portion and a visible one. The latter can be seen from the front attached both above and below to the conjunctiva. On both temporal and nasal surfaces of the visible portion a cavity can be made by the introduction of the forefinger which will enter as far as the first joint; both surfaces are covered by conjunctiva. The living and post-mortem positions of the cartilago are not the same, for the contraction of the retractor muscle after death forces the membrane for a short distance across the cornea.

The larger and more important portion of the cartilago is out of sight and lies embedded in the anterior portion of the large pad of fat found on the inner and inferior aspect of the globe. The following observations refer entirely to the deep or embedded portion of the cartilago. On its temporal surface the cartilago is concave, in order that it may lie against the eyeball; on its nasal surface it is convex, and the most prominent portion of the convexity, which is anteriorly placed about opposite to the origin of the inferior oblique muscle, is covered by a thin layer of pinkish material known as the gland of Harder. This, however, is a very small and unimportant structure in the horse and is difficult to find; moreover, it is not always present. In the eyeball as removed from the socket it is impossible to locate the cartilago at sight; covered by fat it lies in the triangular space formed by the terminal portions of the internal and inferior recti. Even after the fat is removed from its surface it is still impossible to indicate the outline of the cartilago as it runs imperceptibly into the lateral fat pad in which it is lodged. The fat of this body is particularly fibrous and gains a strong attachment to the posterior edge and nasal surface of the cartilago; it is only by perception of the altered resistance offered to the point of the knife that it is possible to say where the cartilago ends and the fat begins. The superior border of the cartilago is accurately defined by the lower edge of the internal rectus muscle which just clears it in order to reach the globe; this muscle gives off stout fascial bands which firmly unite it to the cartilago. There is also a fascial connection, less important, with the inferior rectus muscle. The internal or temporal side of the cartilago is, as above noted, concave in shape for adjustment on the surface of the globe; if the fascial bands derived from the internal rectus muscle be divided, the cartilago can be lifted from the eyeball and its internal surface inspected; this is smooth and forms, with fascial bands from the internal and inferior recti, a bursa between these muscles and the globe, over which the cartilago freely moves; there is practically no fat on the internal surface of the cartilago. Though we have described the cartilago as moving freely in its bursa over the globe, it is actually over one of the insertions of the retractor muscle rather than over the sclerotic itself that the bursal arrangement is placed. The inferior oblique muscle arises about opposite the centre of the cartilago and crosses this structure in such a way as to keep it closely applied to the surface of the eyeball.

LACHRYMAL APPARATUS

The lachrymal gland is a large flat spleen-shaped body about 65 mm. in length and 35 mm. in width. It lies on the upper and temporal side of the eyeball, its tail being uppermost and corresponding in position to about the highest point of the cornea; its head lies low on the outside of the globe about opposite to the outer canthus. How closely this gland is applied to the inner surface of the orbital process will be readily recognised on removing that structure. It fills up the entire space between it and the eyeball, a small portion projecting in front of the orbital process; beneath it is the levator muscle, above it, between the gland and the orbital process, is the periorbita. Numerous nerves enter its posterior edge and large venous plexuses are connected with it both on the upper and the temporal sides of the eyeball. In appearance the gland is greyish-pink in colour and resembles the parotid. Its excretory ducts, which are extremely small, open into the conjunctival sac by minute openings at the outer canthus, but lie a long way back, as deep in fact as where the conjunctiva of the lid is reflected on to the eyeball. In considering this gland one is struck by the large and numerous branches of nerve, by the large venous plexuses present, by the large size of the gland, and by the minute openings of its excretory duct.

The lachrymal puncta in the lids are situated about 2 or 3 mm. above and below the caruncula and lead into the lachrymal ducts. The upper one turns inwards, then bends and runs forwards and downwards behind the caruncula to enter the lachrymal sac which is about 10 mm. below. The lower duct is shorter; it also turns inwards and takes a direct course into the lachrymal sac, lying in almost a horizontal line with it. The ducts and sac are rough internally, the walls being ribbed. The remarkable feature about both ducts and sac is their relatively large size; the ducts are several times larger in diameter than the puncta. The periorbita forms an almost cartilaginous capsule to the sac and a fibrous lining to the nasal canal, while a second layer invests the thick tissues surrounding the canal in its passage to the nasal chamber. The periorbital capsule of the sac is linked up with the caruncula and tissues at the inner canthus of the eye, an arrangement which keeps them firmly in position. The tissues at the inner canthus are accordingly very fibrous.

The lachrymal sac is concave posteriorly and the origin of the inferior oblique fits into the concavity; it is also concave on its temporal side where it is in contact with the fat covering the membrana nictitans. The duct leading from it to the nasal chamber has a remarkably thick corrugated inner wall. The thickness is out of all proportion to the function of the canal, while the actual size of the tear passage is relatively very small. Surrounding the walls of the nasal duct is a vascular plexus, so that the canal to the nasal chamber is much larger than the thick-walled duct it is carrying.

THE EYELIDS

The eyeball is smaller than the orbital cavity, but the presence of a large lachrymal gland above and on the temporal side, together with the existence of a pad of fat on the floor and nasal side, causes the orbit to be completely filled. The cornea projects between the two lids, but as it is placed below the centre of the globe the upper lid is deeper than the lower. The globe is placed so far forward in the orbital cavity that the cornea, iris, ciliary body, and a portion of the lens, are in advance of the bony orbital rim at the canthi. With the head in the normal position the tarsal margin of the upper lid may be 20 mm. and that of the lower lid 13 mm. in front of a vertical dropped from the rim of the orbit.

The skin of the eyelids is generally black, and the pigment extends to the tarsal margin in contact with the globe, where it abruptly ends. The hair on the upper lid is very short, but gradually lengthens in an upward direction and finally runs into the general hair of the face. On the lower lid there is a black shiny hairless surface just below where the scanty eyelashes exist; beneath this the hairs begin to appear in rows, at first very short but gradually increasing in length with each successive row, until the "feelers" are reached, by which time the full length of hair is obtained. The tarsal margin of the lids is relatively thick, the thickest part being midway between the canthi, where it measures about 2 mm. The margin is rounded, shiny, black and hairless; its conjunctival side is closely applied to the eyeball but towards the inner canthus, owing to the presence of the membrana nictitans, it is no longer in contact with the globe.

The eyelashes on the upper lid are large and well developed, excepting at the inner third, which is hairless, and are placed at a distance of about 2 mm. from the inner or conjunctival edge of the lid. There are two or three rows of eyelashes; each row takes a different direction, so that they cross lattice-wise. The longest lashes are centrally placed, and occupy the lowest row; they get progressively shorter in the upper rows. On the lower lid some fine hairs, corresponding to short eyelashes, may be seen, though they are frequently absent.

The upper lid is markedly wrinkled, the result of doing practically all the work, for the movement of the lower lid is very limited; the wrinkling takes a definite pattern, which is accentuated towards the inner third of the upper lid owing to the peculiar shape of the part. The line of the lid is "pulled up" as it were, and then descends by a sharp slope to the lachrymal pool. The lower lid has no such irregularity on its tarsal margin, but forms a semi-circle. Where the two lids meet at the inner canthus there is another hairless black surface also wrinkled which runs outwards towards the face.

The brow is formed by the tissues covering the orbital process; its most prominent point is on the nasal side where a large thick mass exists which is just clear of the eyelid and runs down almost to the inner canthus. The hair

pattern on this prominence is distinctive; it runs upwards in a semi-circular sweep. There are no eyebrows, but large "feelers" exist on the brow which give warning of danger. Similar feelers are found on the lower lid and serve the same purpose. The "feelers" run completely through the skin and each is embedded in a capsule in the orbicularis muscle.

The basis of each eyelid is a layer of periorbita which in the upper lid enters directly, but is differently arranged in the lower. It will be remembered that the periorbita of the orbital process splits at the rim, one portion linking up with the periosteum, the other entering the eyelid. In the lower lid the periosteum and periorbita meet, fuse, and form a crescentic curtain across the orbital opening from one side to the other; it is on the upper edge of this curtain that the true lower lid is built. This crescentic curtain may be as much as 12 mm. in height at its central part and on this another 12 mm. of eyelid is superposed.

The structures found in the lids, detailed from within outwards, are as follows: conjunctiva, levator muscle, periorbita (or in the case of the lower lid a mixed layer of periorbita and periosteum), fascia, orbicularis muscle and skin. In each lid there is a well-marked, relatively thick tarsal cartilage and meibomian glands. The crescentic membrane on which the lower lid is constructed is closely applied to the external face of the fat which lies at the base of the eyeball; into this fat, in order to keep it in position, the membrane sends numerous fibres. The outer face of the elliptical membrane is covered by the orbicularis muscle. Above the layer of fat at the base of the eye, namely between it and the eyeball, is found the fascia which enters the lower lid; it is derived from the inferior rectus muscle.

The lachrymal lake at the inner canthus is constructed in very rigid tissue, composed of skin, muscle and an abundance of fibrous material. The whole of the "corner of the eye" is held firmly in position by the lachrymal ligament which runs from the orbital margin to the lachrymal lake.

The conjunctival sac is deepest in the vicinity of the upper lid, especially at its temporal side, where it extends beneath the orbital process for at least 20 mm. It is also deep on the nasal aspect. In the lower lid it is relatively shallow and limited to the depth of the true eyelid.

The *orbicularis oculi* muscle is a large, flat, oval-shaped structure surrounding the orbit. Over the orbital process and on its nasal side it links up with the *corrugator supercilii* and here the part is very thick and constitutes the marked prominence described in speaking of the brow. With this exception the orbicularis is a flat muscle arranged in layers and possesses an extensive fibrous base due to thickened periosteum or to layers of connective tissue outside the periosteum. It covers a wide area outside the orbital rim and plasters over both upper and lower lids. To the skin of these and the surrounding parts it is so intimately attached that it is impossible to separate the two structures cleanly.

The *corrugator supercilii* is a peculiar muscle arising from the frontal bone.

On contraction it wrinkles or "pinches up" the brow; it does not raise the upper lid.

The *caruncula lachrymalis*, a body the size of a small pea, is deeply pigmented and has a few hairs growing from its surface. On section it is found to be almost wholly glandular, the glands being of the sebaceous and mucous type.

I am greatly indebted to Captain F. C. MINETT, M.B.E., B.Sc., R.A.V.C., and the Authorities of the Royal Army Veterinary School, Aldershot, for the supply of anatomical material for this enquiry,

APPOINTMENT

THE COUNCIL of the University of Birmingham has appointed Dr James Couper Brash to the chair of Anatomy in succession to the late Professor Peter Thompson. Professor Brash became a student demonstrator under Professor D. J. Cunningham in 1908 and later was appointed demonstrator in Pathology under Professor Greenfield. After acting for a short time as demonstrator of Anatomy under Professor Arthur Robinson at Edinburgh, he was appointed assistant to Prof. Kay Jamieson at Leeds in 1911. Holding a Commission in the Special Reserve of the R.A.M.C., he was mobilised, August, 1914, and remained on active service until April, 1919, when he again took up his demonstratorship at Leeds. In October, 1919, he was appointed assistant to Professor Peter Thompson in Birmingham. Here, owing to the state of the Professor's health, the work of the department fell to a great extent on Dr Brash—who carried on, during the two past years, the high traditions established in the University of Birmingham by Windle, Robinson and Thompson. Readers of this Journal are already acquainted with the finished nature of research work which Professor Brash has found time to do in the midst of military and other duties and will be glad to know that he has several investigations now in hand.

INDEX

Allis, Edward Phelps, Jr. The Myodome and the Trigemino-Facialis chamber in the Coelacanthidae, Rhizodontidae and Palaeoniscidae, 149

— The cranial anatomy of Polypterus, with special reference to *Polypterus bichir*, 189

Anencephalic Embryo, Report on, J. Ernest Frazer, F.R.C.S., 12

Appleton, A. B. On the hypotrochanteric fossa and accessory adductor groove of the primate femur, 295

Appointment. James Couper Brash to the Chair of Anatomy, University of Birmingham, 390

Arvicola (*Microtus*) *Amphibius*, early development and placentation in, with special reference to the origin of placental giant cells. By G. S. Sansom, B.Sc., 333

Aspermatic condition of the imperfectly descended Testis, suggestion as to the cause of. By F. A. E. Crew, M.D., D.Sc., 98

Blair, Duncan M., M.B., Ch.B. A Note on the Post-coronal Sulcus, with dissections of the Epicranial Aponeurosis in two cases of its occurrence, 44

Bolk, L., M.D. Odontological Essays, 107

Bones in the palate and upper jaw of the fishes, a new interpretation of. By H. Leighton Kesteven, D.Sc., M.D., Ch.M., 307

Brash, James Couper, appointed to Chair of Anatomy, University of Birmingham, 390

Braus, Hermann, Anatomie des Menschen: ein Lehrbuch für Studierende und Ärzte, Review, 161

Bresslau, Ernst. The Origin of Milk Glands: The Mammary Apparatus of the Mammalia, in the Light of Ontogenesis and Phylogenesis. Review, 55

Coelacanthidae, Rhizodontidae, and Palaeoniscidae, Myodome and the Trigemino-Facialis chamber in. By Edward Phelps Allis, Jr., 149

Colons, Iliac and Pelvic, abnormal position of. By Naguib Effendi Nicola, 53

Crew, F. A. E., M.D., D.Sc. A suggestion as to the cause of the aspermatic condition of the imperfectly descended Testis, 98

Cyriax, Edgar F., M.D. (Edin.). On certain normal irregularities in the Vertebral Column in its lower dorsal area, 147

Dart, Raymond A., M.Sc., M.B., Ch.M. and Joseph L. Shellshear, M.B., Ch.M. The Origin of the Motor Neuroblasts of the Anterior Cornu of the Neural Tube, 77

Dart, Raymond A., M.Sc., M.B., Ch.M. The misuse of the term "Visceral," 177

Das, Basanta Kumar, M.Sc. (Allahabad). On truncated umbilical arteries in some Indian mammals, 325

Dilworth, T. F. M., M.B., B.Ch. The Nerves of the human larynx, 48

Embryo, Anencephalic, Report on, J. Ernest Frazer, F.R.C.S., 12

— human, absence of the lens occurring in. By Ida C. Mann, M.B., B.S., 96

— of Lygosoma, skull and some related structures of. By Helga S. Pearson, B.Sc., 20

Epicranial Aponeurosis, Note on the Post-Coronal Sulcus, with dissections of. By Duncan M. Blair, M.B., Ch.B., 44

Eye of horse, anatomical notes of the accessory organs of. By Sir Frederick Smith, K.C.M.G., C.B., 366

Femur, mammalian, correlation between Habit and the Architecture of. By G. de M. Rudolf, M.R.C.S. (Eng.), L.R.C.P. (Lond.), D.P.H., 137

— of primate, hypotrochanteric fossa and accessory adductor groove of. By A. B. Appleton, 295

Fishes, a new interpretation of the bones in the palate and upper jaw of. By H. Leighton Kesteven, D.Sc., M.D., Ch.M., 307

Foetus, human, exhibiting Iniencephaly and other abnormalities. By William Ivon Hayes, M.B. (Melb.), 155

Frazer, J. Ernest, F.R.C.S., Report on an Anencephalic Embryo, 12

Habit and the Architecture of the mammalian femur, correlation between. By G. de M. Rudolf, M.R.C.S. (Eng.), L.R.C.P. (Lond.), D.P.H., 137

Hayes, William Ivon, M.B. (Melb.). A human Foetus exhibiting Iniencephaly and other abnormalities, 155

Herrick, C. Judson, What are viscera? 167

Horse, eye of, anatomical notes of the accessory organs of. By Sir Frederick Smith, K.C.M.G., C.B., 366

Hunter, John I., M.B., Ch.M. A case of early human Ovarian Pregnancy, 57

Hypotrochanteric fossa and accessory adductor groove of the primate femur. By A. B. Appleton, 295

Iliac and Pelvic colons, abnormal position of. By Naguib Effendi Nicola, 53

Indian mammals, truncated umbilical arteries in. By Basanta Kumar Das, M.Sc. (Allahabad), 325

Iniencephaly and other abnormalities, human Foetus exhibiting. By William Ivon Hayes, M.B. (Melb.), 155

Interphalangeal and Metacarpo-Phalangeal Joints, Nerve supply of. By John S. B. Stopford, M.D., 1

Jaw, upper, of fishes, a new interpretation of the bones in the palate and. By H. Leighton Kesteven, D.Sc., M.D., Ch.M., 307

Joints, Interphalangeal and Metacarpo-Phalangeal, Nerve supply of. By John S. B. Stopford, M.D., 1

Kesteven, H. Leighton, D.Sc., M.D., Ch.M. A new interpretation of the bones in the palate and upper jaw of the fishes, 307

Kidd, Walter, M.D., F.R.S.E. Initiative in Evolution, Review, 55

Larynx, human, Nerves of. By T. F. M. Dilworth, M.B., B.Ch., 48
Lens, absence of, occurring in the human embryo. By Ida C. Mann, M.B., B.S., 96
Lygosoma, Embryo of, Skull and some related structures of. By Helga S. Pearson, B.Sc., 20

Mann, Ida C., M.B., B.S. Absence of the lens occurring in the human Embryo, 96
Metacarpo-Phalangeal and Interphalangeal Joints, Nerve supply of. By John S. B. Stopford, M.D., 1
Myodome and the Trigemino-Facialis chamber in the Coelacanthidae, Rhizodontidae and Palaeoniscidae. By Edward Phelps Allis, Jr., 149

Nerve supply of the Interphalangeal and Metacarpo-Phalangeal Joints. By John S. B. Stopford, M.D., 1
Nerves of the human larynx. By T. F. M. Dilworth, M.B., B.Ch., 48
Neural Tube, origin of the Motor Neuroblasts of the Anterior Cornu of. By Raymond A. Dart, M.Sc., M.B., Ch.M. and Joseph L. Shellshear, M.B., Ch.M., 77
Neuroblasts, Motor, of the Anterior Cornu of the Neural Tube, Origin of. By Raymond A. Dart, M.Sc., M.B., Ch.M. and Joseph L. Shellshear, M.B., Ch.M., 77
Nicola, Naguib Effendi, Abnormal position of the Iliac and Pelvic colons, 53

Obituary notice of Dr Peter Thompson. By Arthur Robinson. Portrait, 164
Odontological Essays. By L. Bolk, 107

Palaeoniscidae, Coelacanthidae and Rhizodontidae, Myodome and the Trigemino-Facialis chamber in. By Edward Phelps Allis, Jr., 149
Palate and upper jaw of the fishes, a new interpretation of the bones of. By H. Leighton Kesteven, D.Sc., M.D., Ch.M., 307
Pearson, Helga S. The Skull and some related structures of a late Embryo of Lygosoma, 20
Pelvic and Iliac Colons, abnormal position of. By Naguib Effendi Nicola, 53
Placentation and development in *Arvicola* (*Microtus*) *Amphibius*, with special reference to the origin of placental giant cells. By G. S. Sansom, B.Sc., 333
Polypterus, cranial anatomy of, with special reference to *Polypterus bichir*. By Edward Phelps Allis, Jr., 189
Post-Coronal Sulcus, with dissections of the Epicranial Aponeurosis in two cases of its occurrence. By Duncan M. Blair, M.B., Ch.B., 44
Pregnancy, Ovarian, Case of early human. By John I. Hunter, M.B., Ch.M., 57

Reviews. Anatomie des Menschen: ein Lehrbuch für Studierende und Ärzte. By Hermann Braus, 161
— Hereditary disease. By Hermann W. Siemens, 162
— Initiative in Evolution. By Walter Kidd, M.D., F.R.S.E., 55
— Studies in the Palaeopathology of Egypt. By Sir Marc Armand Ruffer, C.M.G., M.D., 160
— The Origin of Milk Glands: The Mammary Apparatus of the Mammalia, in the light of Ontogenesis and Phylogenesis. By Ernst Bresslau, M.D., 55
Rhizodontidae, Coelacanthidae, and Palaeoniscidae, Myodome and the Trigemino-Facialis chamber in. By Edward Phelps Allis, Jr., 149
Robinson, Arthur. Obituary notice of Dr Peter Thompson. Portrait, 164
Rudolf, G. de M., M.R.C.S. (Eng.), L.R.C.P. (Lond.), D.P.H. Correlation between Habit and the Architecture of the Mammalian Femur, 137
Ruffer, Sir Marc Armand, C.M.G., M.D. Studies in the Palaeopathology of Egypt, Review, 160

Sansom, G. S., B.Sc. Early development and placentation in *Arvicola* (*Microtus*) *Amphibius*, with special reference to the origin of the placental giant cells, 333
Shellshear, Joseph L., M.B., Ch.M. and Raymond A. Dart, M.Sc., M.B., Ch.M. The Origin of the Motor Neuroblasts of the Anterior Cornu of the Neural Tube, 77
Siemens, Hermann W. Hereditary disease, Review, 162
Skull and some related structures of a late Embryo of Lygosoma. By Helga S. Pearson, B.Sc., 20
— Post-Coronal Sulcus of, with dissections of the Epicranial Aponeurosis in two cases of its occurrence. By Duncan M. Blair, M.B., Ch.B., 44
Smith, Sir Frederick, K.C.M.G., C.B. Anatomical notes on the accessory organs of the eye of the horse, 366
Stopford, John S. B., M.D. Nerve supply of the Interphalangeal and Metacarpo-Phalangeal Joints, 1
Sulcus, Post-Coronal, with dissections of the Epicranial Aponeurosis in two cases of its occurrence. By Duncan M. Blair, M.B., Ch.B., 44

Testis, imperfectly descended, suggestion as to the cause of the aspermatic condition of. By F. A. E. Crew, M.D., D.Sc., 98
Thompson, Dr Peter. Obituary notice of. By Arthur Robinson, Portrait, 164
Trigemino-Facialis Chamber and Myodome in the Coelacanthidae, Rhizodontidae and Palaeoniscidae. By Edward Phelps Allis, Jr., 149

Umbilical arteries, truncated, in some Indian mammals. By Basanta Kumar Das, M.Sc. (Allahabad), 325

Vertebral column in its lower dorsal area, certain normal irregularities in. By Edgar F. Cyriax, M.D. (Edin.), 147
Viscera, What are Viscera? By C. Judson Herrick, 167
"Visceral," misuse of term. By Raymond A. Dart, M.Sc., M.B., Ch.M., 177